Towards ecosystem-based management of Tasmanian temperate rocky reefs: Community dynamics models indicate alternative community states and management strategies

Martin Pierre Marzloff
M.Sc.

Submitted in fulfilment of the requirements for the Degree of
Doctor of Philosophy in Quantitative Marine Science
(A joint CSIRO & UTas Ph.D. program in quantitative marine science)
at the University of Tasmania.

Institute for Marine and Antarctic Studies (IMAS), University of Tasmania
July 2012

Declarations

Statement of originality

I declare that this thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

Signed:  (Martin Pierre Marzloff)

Date: 3th July 2012

Statement of accessibility

This thesis may be made available for loan and limited copying in accordance with the *Copywright Act of 1968*

Signed:  (Martin Pierre Marzloff)

Date: 3th July 2012

Abstract

Worldwide, ecosystems have demonstrated the potential for dramatic shifts to an alternative persistent state under gradual long-term environmental changes or following sudden short-term perturbations. Such shifts are documented for numerous marine examples from coral reef to pelagic communities and may become more common as ecological dynamics adjust to climate-driven changes. These shifts are often sudden, challenging to predict and can have disastrous and unpredictable consequences on both ecosystem functioning and the human activities that rely on the associated natural resources. They often result in irreversible dramatic changes in community structure and productivity and represent a growing concern for managers of natural systems.

In ecosystems where the presence of an alternative persistent state is well documented, the drivers of these shifts (e.g. anthropogenic stressors or changes in environmental conditions) can be analysed retrospectively so as to address key management questions, as has occurred in several applications on coral reefs. However, phase shifts are often swift and observed *a posteriori*, i.e. after the ecosystem has shifted to the alternative state. Thus, thresholds in ecosystem dynamics are difficult to identify empirically despite that this is crucial for sound management of marine resources. Additionally, controlled experimental assessment of the effects of alternative management scenarios on community state is hardly ever achievable in marine ecosystems. When they occur, phase shifts are unique to each ecosystem, hence case-specific simulation models present a valuable tool to explore ecological dynamics with alternative persistent community states, test the effects of management scenarios and inform decision-making.

On the east coast of Tasmania, shallow rocky reef communities on the exposed coast mainly occur in two alternative persistent states: (1) the seaweed bed state characterised by a dense productive canopy of macroalgae; or, (2) the sea urchin 'barren' state characterised by a poorly productive rocky habitat largely bare of seaweeds as a result of destructive grazing by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of

these widespread sea urchin barrens result from a combination of both: (1) the climate-driven range extension of the long-spined sea urchin *C. rodgersii* from Australia's mainland to Tasmania; and (2) depletion of key reef predators by fishing. Large southern rock lobster (*Jasus edwardsii*) individuals constitute the main predator of the long-spined sea urchin in Tasmania. Relative to the seaweed bed state, *C. rodgersii* barrens represent dramatic losses of habitat, species diversity and productivity, including commercial species such as blacklip abalone (*Haliotis rubra*) and southern rock lobster, the two most valuable fisheries in Tasmania. Thus, the spread of sea urchin barrens presents a major and pressing threat for the lobster and abalone fishing industries.

This thesis presents a suite of models specifically developed to better understand the dynamics of Tasmanian rocky reef communities and inform management interventions to mitigate destructive grazing of seaweed beds by the invasive long-spined sea urchin.

Chapter 2 investigates the causal relationships between positive feedback and the occurrence of alternative states in community dynamics. Modelling of community feedback informed by available qualitative knowledge about ecosystem structure constitutes a valuable framework to detect the potential for alternative states in ecological dynamics as illustrated with some examples from Tasmanian rocky reef communities. Qualitative modelling assists to understand the essential features of temperate reef dynamics around Tasmania, and provides a useful first step towards quantitative modelling of rocky reef dynamics. The approach provides an ideal framework to (i) collate all available information about rocky reef ecology, (ii) test model structure uncertainty, and (iii) identify key drivers of alternative states in ecosystem dynamics.

The quantitative model presented in the subsequent chapters captures the dynamics of the three key groups or species (i.e. the rock lobster, sea urchin, and seaweed assemblage) directly involved in the positive feedback that drives the shift between alternative states on Tasmanian rocky reef. **Chapter 3** describes the development, parameterisation and calibration of a mean field model of the local dynamics (reef area of 100 m^2 - 10 ha) of a reef community. The model's ability to capture the potential for phase shifts, from dense seaweed bed to sea urchin barrens habitat and back, is validated against large-scale patterns observed on rocky reefs where *C. rodgersii* occurs. In the simulations, the time for extensive sea urchin barrens to form is of the order of two decades, while

restoration of seaweed cover from the sea urchin barrens habitat takes about three decades if relying on management interventions that cannot effectively reduce urchin density to zero. Thus, restoration of seaweed beds seems unrealistic to implement within the current timeframe of management plans. Comprehensive model-independent sensitivity analysis of model behaviour to parameter estimates also suggests that, in addition to lobster fishing mortality, recruitment rates of sea urchins and rock lobsters, which are strongly influenced by large scale oceanographic features and highly variable in eastern Tasmania, are key factors in determining the potential for sea urchin barren formation in the model.

In **Chapter 4**, sets of Monte-Carlo simulations with this model are used to address three sets of questions related to management for mitigation of sea urchin destructive grazing of Tasmanian seaweed beds. Model behaviour suggests that thresholds in shifting from seaweed bed to sea urchin barren and restoration of seaweed cover reveal the existence of a hysteresis in model dynamics. The hysteresis implies that the establishment of sea urchin barrens cannot be reversed easily. These thresholds provide valuable ecological reference points to prevent the establishment of sea urchin barrens. The model indicates that culling of sea urchins appears as the most effective management strategy to minimise the ecological impact of *C. rodgersii* on Tasmanian reef communities. Indirect interventions relying solely on the rebuilding of rock lobster population (through reduction in fishing or implementation of a maximum legal catch size) perform poorly but, when combined with direct control of the sea urchin population, they can provide optimal outcomes both in terms of minimising barren formation and fishery performance. Finally, the model shows that to allow lobsters to play their critical ecological 'service' role in preventing sea urchin barrens formation, a reduction in lobster fishing mortality from current levels is required. A maximum sustainable yield as estimated from the single species stock assessment model does not account for the ecosystem service delivered by larger lobsters, and the models emphasise the need for an ecosystem-based fishery management approach.

This suite of models contributes to the general understanding of mechanisms and drivers that can facilitate shift between alternative states in ecological dynamics. The quantitative simulation model provides specific information to managers about the drivers of shifts between the seaweed bed and the sea urchin barren state in the dynamics of Tasmanian rocky reefs. In particular, the presence of a hysteresis in reef community dynamics means that effort to prevent barrens formation constitutes a more viable and cost effective

management strategy than the restoration of seaweed beds once extensive barrens habitat has developed. The commercially-fished rock lobster is an essential reef predator delivering key ecosystem services to Tasmanian rocky reefs and model simulations highlight the necessity for fisheries management to move away from a single species focus and account for the ecological role of targeted commercial species. The tools implemented here to inform an ecosystem-based management of Tasmanian rocky reefs are generic and 'transportable' to other ecosystems with alternative states. While *C. rodgersii* barrens currently constitute a pressing concern for managers of reef communities and fisheries in Tasmania, the long-spined sea urchin is only one example of a species that is dramatically restructuring Tasmanian reef communities. There are many other 'natural' invaders, whose ecosystem roles and impacts are unknown, currently extending their distribution from Australia's mainland to the warming Tasmanian waters. In the coming decades, climate-driven changes are likely to bring more surprises to Tasmanian rocky reefs, and just as many challenges for the associated fisheries and their managers.

Contents

List of Figures

List of Tables

Acknowledgements

First, I would like to thank my supervisors, Prof. Craig Johnson, Dr. Rich Little and Ass. Prof. Stewart Frusher, for giving me the opportunity to tackle this exciting and innovative project. Thanks for the enthusiastic discussions, for your constructive and thought-provoking feedback, for your patience, support and guidance along the way.

Thanks to those who contributed to part of this Ph.D. journey. I am very grateful to Dr. Jeffrey Dambacher for his involvement at the start of my project, for the passionate and inspiring discussions about qualitative modelling, positive feedback and alternative states and for his precious mentoring as developing and writing up Chapter 2. Thanks to Dr. Jean-Christophe Soulié for his time and his warm and welcoming attitude on each of my visits back in France at CIRAD, Montpellier; for his guidance to develop the Python code and to set up the sensitivity analysis tools behind Chapters 3 and 4; for making each of these computer-programming sessions instructive, fun and very enjoyable. Many thanks to Dr. Scott Ling for sharing his understanding of Tasmanian reef ecology and for the valuable discussions as chasing up the best parameter estimates for the simulation model of Tasmanian rocky reef community dynamics developed in Chapter 3 .

I am very thankful to the joint UTas - CSIRO Ph.D. programme in Quantitative Marine Science that supported most of my Ph.D. research and gave me some unique exposure to loads of exciting ideas and passionate marine scientists around Hobart as completing my research. My four-year enrolment as an international student at the University of Tasmania was supported by an Endeavour International Postgraduate Research Scholarship. The Wealth from Ocean Flagship co-funded my Ph.D. and supported my attendance at several workshops and conferences, both around Australia and overseas. I was also the recipient of a 2009 Tasmanian Marine Science Fellowship that supported a 3-month visit to France to collaborate with Jean-Christophe Soulié (CIRAD).

Thanks to the fisheries science department in Rennes for kindling my interests in marine and fisheries science. To Dr. Yunne-Jai Shin who first opened up my mind to the exciting world of marine ecosystem modelling.

Thanks to my family for cultivating my love of the Ocean. Thanks to the North Sea and its fishers for being inspiring next door neighbours and to Belle-Isle-En-Mer and the Atlantic Ocean for being magic playgrounds as growing up. Thanks to all the friends who shared the ups and downs of this Ph.D. journey, for feeding me good food when hungry and good distractions (surfing, sailing, bushwalking, fishing adventures) as often as possible. Special thanks to Katherine for giving me a good reason to come back to Tasmania, for her support through the wanders at the start of my Ph.D. To Pier for the faithful companionships to chase waves. To Meme for the best outdoorsy distractions and other escapes into Tasmania's wilderness. To Sjoerd for the entertaining coffee breaks and regular lunchtime runs during the last few months of this project. To Pip for the productive and fun 'Ph.D. writing retreats' away from Hobart's distractions. To Yannick for the visit and good mentoring as writing up. Thanks for all the good music that often fed my inspiration and productivity while in the office.

To Malou Zuidema for the Tasmanian reef artwork on the cover of this thesis.

Final thanks go to Dr Morgane Travers-Trolet and Dr Anne Salomon for providing some helpful and constructive comments on the original version of this thesis.

Statement of co-author contributions

Prof. Craig Johnson (UTas) provided comments on the general sections of this thesis (**Chapters 1 and 5**).

Chapters 2 - 4 of this thesis have been prepared as manuscripts for submission to peer-reviewed journals. In all cases the design and implementation of the research, data analysis, interpretation of results and manuscript preparation were the responsibility of the candidate but were carried out in consultation with supervisors and with input from specialist contributors. These contributions are outlined for each of these chapters below.

Chapter 2: Dr. Jeffrey Dambacher (CSIRO), Prof. Craig Johnson (UTas) and Dr. Rich Little (CSIRO) contributed to the development of the ideas. Dr. Jeffrey Dambacher provided technical advice on qualitative modelling of complex systems' feedback. Prof. Craig Johnson, Ass. Prof. Stewart Frusher (UTas), Dr. Scott Ling (UTas), Dr. Elizabeth Strain (UTas) provided background knowledge about Tasmanian reef ecology. Contributing authors, as well as Dr. Elizabeth Fulton (CSIRO), Dr. Geoffrey Hosack (CSIRO) and two anonymous reviewers, provided comments on the manuscript.

Published as: Marzloff, M.P., Dambacher, J.M., Johnson, C.R., Little, L.R. and Frusher, S.D., 2011. Exploring alternative states in ecological systems with a qualitative analysis of community feedback. Ecological Modelling, 222: 2651-2662.

Chapter 3: Prof. Craig Johnson (UTas), Dr. Rich Little (CSIRO) and Dr. J.-C. Soulié (CIRAD) provided advice on model development and approaches for sensitivity analysis. Prof. Craig Johnson, Dr. Scott Ling (UTas) and Ass. Prof. Stewart Frusher (UTas) provided some advise on model parameterisation. Prof. Craig Johnson, Dr. Scott Ling, Dr. Neville Barrett (UTas), Dr. Graham Edgar (UTas), Ass. Prof. Stewart Frusher, Dr. Klaas Hartman (UTas), Dr. Caleb Gardner (UTas), Ph.D. candidate Kevin Redd (UTas) provided data to define model parameterisation. Prof. Craig Johnson, Dr. Scott Ling and Dr. Rich Little provided comments on the manuscript.

Manuscript prepared for submission to Ecological Modelling as: Marzloff, M.P., Johnson, C.R., Little, L.R., Ling S.D. and Soulié, J.-C. Pattern-oriented validation and sensitivity analysis of a model with alternative community states: A simulation model of ecological dynamics of temperate rocky reefs in Tasmania.

Chapter 4: Prof. Craig Johnson and Dr. Rich Little provided advice on scenario testing. Contributing authors provided comments on the manuscript.

Manuscript prepared for submission to Ecological Applications as: Marzloff, M.P., Johnson, C.R. and Little, L.R. Alternative states on Tasmanian rocky reefs: Identifying thresholds in community dynamics and assessing management interventions to limit destructive grazing of sea urchins.

Chapter 1 Introduction

"Variability is normality." Valdivia (1978) about the northern Humboldt ecosystem following the 1973 collapse of the world champion Peruvian anchoveta fishery.

Variability across a range of scales in space and time is a key characteristic of ecological dynamics (Doak et al., 2008), underpinned by a suite of disparate causal mechanisms. Beyond short-term variability of natural dynamics (e.g. seasonal or interannual), environmental or anthropogenic perturbations can facilitate sudden shifts between alternative persistent community states (May, 1977; Scheffer et al., 2001; Beisner et al., 2003; Scheffer and Carpenter, 2003). In these cases, ecological communities can manifest 'phase shifts' in which large changes in species abundances are observed without any tendency to return to the previous configuration (Scheffer et al., 2001). Alternative states have been reported both in terrestrial and aquatic systems (Schroder et al., 2005), and shifts from one state to another can be continuous or discontinuous (Scheffer et al., 2001; Beisner et al., 2003). Discontinuous transitions represent ecological hysteresis, i.e. dynamics where a small change in parameters or species abundance can lead to a dramatic shift to a new community state that persists when the change is reversed (Donahue et al., 2011). However, detailed observations of this kind of transition in nature are scarce, in particular for communities with hysteresis. Indeed, such ecosystems (e.g. coral reefs or eutrophic lakes) are commonly described as in one community state or the other with some limited understanding of the actual transition dynamics (Scheffer et al., 1993; Scheffer and Carpenter, 2003). These shifts in community dynamics can dramatically alter ecosystem functioning and have disastrous consequences on the human activities that rely on use of natural resources (Scheffer et al., 2001). Phase shifts are challenging to anticipate and their consequences difficult to predict (Scheffer and Carpenter, 2003; Doak et al., 2008). While natural variability implies constant changes in environmental conditions (seasonal and interannual variability in environmental conditions), which make ecological dynamics difficult to predict (Doak et al., 2008) and the management of natural

resources uncertain (e.g. years of low recruitment in fishery management), it can lead with no warning to dramatic changes in ecosystem functions and structure in dynamics with alternative states (Hastings and Wysham, 2010). Thus, detecting the potential for alternative states in ecosystems and better understanding these dynamics and their drivers are essential to maintain ecosystem well functioning and avoid the unpredictable consequences of discontinuous ecosystem shifts (van de Koppel et al., 1997; de Young et al., 2008; McClanahan et al., 2011).

Two main types of perturbations can alter the state of an ecosystem: 1) a sudden stochastic event that modifies state variables on short time scales (e.g. an extreme weather event that causes a dramatic mortality event for a population) and 2) a sustained external constraint (e.g. fishing pressure) that affects population growth rates (birth, mortality or migration) over long time scales (Scheffer et al., 2001; Beisner et al., 2003). There has been a resurgence of interest in phase shift theory over the last few decades (Petraitis and Dudgeon, 2004) as the effects of human activities on ecosystems become better understood (Scheffer et al., 2005; de Young et al., 2008; Ling et al., 2009*a*). Human-induced stresses on ecosystems can be categorised arbitrarily into two groups: 1) large scale atmospheric and oceanographic changes (e.g. as a result of anthropogenic carbon emissions) can affect most components of ecosystems, from the physical environment (e.g. temperature) to animal physiology (Cury et al., 2008; Running, 2008; Overland et al., 2010; Johnson et al., 2011); and 2) local human activity through direct exploitation of natural resources (e.g. fishing) or indirect human inputs (e.g. pollution) that can significantly affect the local natural environment (Scheffer et al., 2005; Edgar et al., 2009). The effects of both global climate-driven changes and local human activities can potentially have dramatic consequences on the dynamics of ecosystem with alternative persistent state as they can facilitate sudden shift to a less desirable ecosystem state (Scheffer and Carpenter, 2003; Genkai-Kato, 2007). Thus, better understanding anthropogenic as well as environmental drivers of phase shifts have become a major concern for the sound management of ecological systems (Folke et al., 2004; Genkai-Kato, 2007; de Young et al., 2008).

Because phase shifts are often swift, evidence for alternative states in nature are typically collated *a posteriori*, i.e. once a community has shifted to an alternative state and the dramatic consequences of a shift are observed (Scheffer et al., 2005; Ling et al., 2009*a*). While there exists a body of theoretical literature about alternative states and phase

shifts, demonstrating their existence in natural systems (de Young et al., 2004; Petraitis and Dudgeon, 2004), characterising the nature of the anthropogenic and/or environmental drivers of these shifts (Scheffer and Carpenter, 2003), identifying key thresholds in ecological dynamics that manifest hysteresis (McClanahan et al., 2011), and predicting their effects on ecosystem function, each constitute major challenges for ecologists and for the robust management of human activities in systems with the capacity for rapid phase shift (de Young et al., 2008; Overland et al., 2008). Moreover, these features are also difficult to assess experimentally (Petraitis and Dudgeon, 2004). In particular, controlled experimental testing of the long-term effects of alternative management scenarios is effectively hard to achieve in 'real world' ecosystems (Scheffer and Carpenter, 2003). Therefore, mathematical models, albeit difficult to parameterise and validate, have a central role in helping to predict and understand alternative states in ecosystems where anthropogenic effects can lead to dramatic irreversible changes (Scheffer et al., 2001; Mumby et al., 2007; Firn et al., 2010; Melbourne-Thomas et al., 2010; Estes et al., 2011; Fung et al., 2011; McClanahan et al., 2011). Phase shifts are unique to each ecosystem, and so case-specific simulation models present a valuable tool to (i) explore ecological dynamics in which there are possible alternative community states, (ii) test the effects of management scenarios, and (iii) inform decision making (Scheffer and Carpenter, 2003; de Young et al., 2008). Several ecological models of marine ecosystems with potential alternative community states have been developed in recent years and applied usefully to management support of real ecosystems (see Mumby et al., 2007; Melbourne-Thomas et al., 2010 for some coral reef examples).

On the east coast of Tasmania in southeastern Australia (cf. map given in Fig. 1.1), shallow (< 35 m depth) exposed rocky reef communities mainly occur in two alternative persistent states: (1) the seaweed bed state characterised by a dense productive canopy of macroalgae; or, (2) as sea urchin 'barrens' habitat characterised by a poorly productive and bare rocky habitat following destructive grazing by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of these widespread sea urchin barrens in eastern Tasmania results from a combination of (1) climate-driven range extension of the long-spined sea urchin *C. rodgersii* from Australia's mainland to Tasmania via strengthening eddy activity associated with southern incursions of the tropical East Australian Current (Ling et al., 2009*b*); and (2) the depletion of key predators of the sea urchin by fishing. Large southern rock lobster (*Jasus edwardsii*) individuals constitute

the only effective predator of the long-spined sea urchin in Tasmania (Ling et al., 2009*a*). Sea urchin barrens are observed in many temperate regions around the globe (Lawrence, 1975; Mann, 1982; Chapman and Johnson, 1990; Steneck et al., 2004) and constitute an impoverished state compared to productive macroalgal beds in terms of productivity, complexity of habitat and species diversity (Ling, 2008). Since the 1980s, sea urchin barrens up to 10-50 ha in extent have become established in exposed shallow-water regions on the northeast coast of Tasmania as a consequence of destructive grazing by *Centrostephanus rodgersii* (Johnson et al., 2005; Ling et al., 2009*a*). Amongst other Tasmanian reef species, high-value blacklip abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*) fisheries, with a combined value of about AUD$150M pa, severely decline on urchin barrens (Johnson et al., 2005).

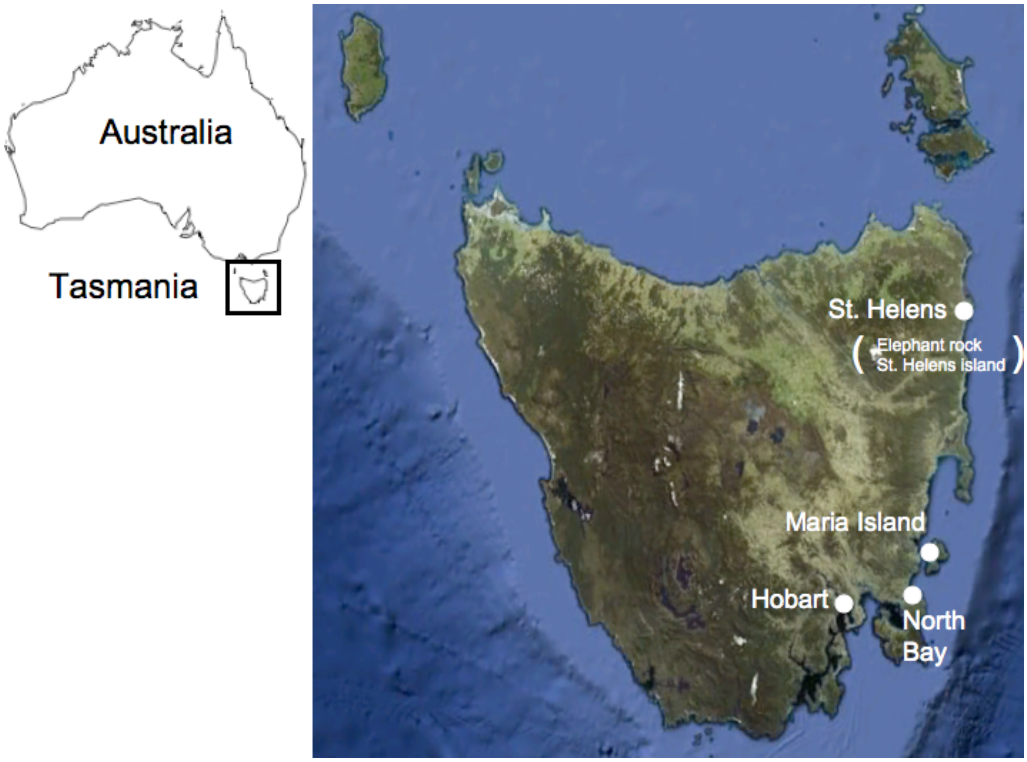


Figure 1.1: Map of Tasmania with the key sites mentioned in the thesis. The top left corner shows the position of Tasmania in the southeastern corner of Australia. Map credits: Google Earth.

The spread of extensive *C. rodgersii* barren is regarded as a principal threat to rocky reef fisheries in eastern Tasmania (Johnson et al., 2005; Pecl et al., 2009; Johnson et al., 2011). However fisheries management is single-species-oriented and does not account for the

ecological impacts of *C. rodgersii*. On Tasmanian rocky reefs, manipulative experiments to examine effects of fishing have been carried out at small scales (e.g. 0.25x0.25m to 4x4m plots in Strain, 2009; Strain and Johnson, 2012). While these studies help to refine understanding of the ecology of individual species (e.g. Ling et al., 2009*b*) and a limited number of pairwise interactions (e.g. Strain, 2009), we lack the practical ability to carry out controlled experiments at a complexity and scale sufficiently large to understand how these species and interactions affect the dynamics of the larger system (Schroder et al., 2005). In particular, there is currently no framework to inform management interventions so as to mitigate the ecological effects of *Centrostephanus rodgersii* invasion along the east coast of Tasmania.

This thesis presents a suite of 'minimum realistic' ecological models (Fulton et al., 2003*a*) developed within the boundaries of current knowledge of Tasmanian reef ecology (empirical observations, results of manipulative experiments or existing models; e.g. Punt and Kennedy, 1997; Johnson et al., 2005; Guest et al., 2009; Ling et al., 2009*a*; Strain, 2009). These models are specifically designed to capture the potential for alternative community states characterised as either dense, diverse and productive stands of macroalgae, or poorly productive sea urchin barrens following destructive grazing of macroalgal beds by *C. rodgersii*. The art of building robust, reliable and hence useful ecosystem models lies in making a series of fine choices, which can be difficult to objectively assess (Klepper, 1997). The three primary chapters of this thesis (Chapters 2-4) describe a set of approaches to step-by-step (i) collate and synthesise available information about rocky reef ecology, (ii) develop, parameterise, test and validate a parsimonious simulation model of Tasmanian reef dynamics with alternative community states, and (iii) identify thresholds in ecosystem dynamics and inform effective management interventions.

Through qualitative modelling of community responses to long-term perturbations, Chapter 2 explores and defines generic mechanistic links between positive feedback and the occurrence of alternative states. Positive feedback diminishes a system's overall resistance to change, and can create and maintain correlations in the relative abundance of variables that coincide with alternative states. With specific models of the dynamics of Tasmanian rocky reef communities, which capture effects of climate change, fishing and persistent alternative states, we demonstrate the ability of qualitative modelling to predict the potential for alternative states in ecosystems and thus identify this possibility

to managers and inform management intervention. We show that qualitative knowledge of community structure permits a thorough analysis of system feedback and an assessment of the potential for an ecosystem to exhibit alternative states.

While they may be deemed as essential to support decision-making, robust simulation models of ecosystems with alternative states are nonetheless challenging to build, test and validate. Chapter 3 develops TRITON (Temperate Reefs In Tasmania with lObsters and urchiNs), a model of the local dynamics of seaweed-based reefs with alternative community states, and presents simulation-based calibration and analyses of model sensitivity to input parameters. Pattern-Oriented-Modelling, i.e. comparing patterns emerging from model dynamics across Monte-Carlo simulations with large-scale observations of Tasmanian reef communities, provides a valuable approach to validate the dynamics of TRITON. Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test (Saltelli et al., 1999), we rank the influence of key parameters on different aspects of model behaviour. The model validation exercise contributed to both (i) a better understanding of the key drivers of Tasmanian rocky reef dynamics (e.g. fishing of rock lobster), and (ii) identification of priority areas for further work through assessment of model limitations stemming from incomplete knowledge of seaweed-sea urchin-lobster dynamics.

In Chapter 4 we address a range of questions for the management of Tasmanian reef communities using Monte-Carlo simulations with TRITON. First, we use the simulations to help characterise thresholds in community dynamics. These tipping points constitute essential reference points for management to minimise the risk of barrens formation or facilitate the recovery of seaweed beds from the barren state, but it is difficult to directly observe them empirically (see Mumby et al., 2007 for a model-based derivation of thresholds in coral reef dynamics). Distinct differences in community thresholds for the "forward' shift' (i.e. barrens formation from high seaweed cover) and "backward' shift' (i.e. recovery of seaweed cover from the barrens condition) reflect a hysteresis in reef dynamics; once sea urchin barrens have formed extensively, restoration of dense seaweed beds is much more difficult to achieve than prevention of barren formation in the first place. Alternative management scenarios (i.e. a combination of reducing lobster fishing, implementing a maximum legal catch size to protect large lobster individuals as key reef predators, culling of sea urchins and translocating large lobsters from deep to shallow reefs exposed to destructive sea urchin grazing) are assessed both in terms of mitigating the ecological

effects of sea urchin grazing and lobster fishery performance. Model simulations highlight the need for the Tasmanian rock lobster fishery management objectives to move away from a single-species-oriented maximum sustainable yield towards a more conservative ecologically sustainable yield that accounts for the ecosystem services delivered by rock lobster to rocky reef communities.

The General Discussion (Chapter 5) summarises all key findings, illustrates the complementarity of the different approaches applied in this thesis to comprehend the dynamics of Tasmanian rocky reefs, including the risks of moving between alternative community states, and attempts to inform an ecologically sound management of the Tasmanian southern rock lobster fishery. Over the last two decades, fisheries scientists have emphasised the necessity to better account for the ecosystem effects of fishing and to shift management practises away from the traditional single species focus towards an ecosystem-based approach (Cury et al., 2005; Smith et al., 2007, 2011). With this simple example from Tasmanian rocky reefs, on which rock lobsters exert essential predation control on sea urchins, we illustrate some of the misleading assumptions of single-species management in circumstances in which the target species delivers key services to the ecosystem. We highlight the need for fishery management targets, such as maximum sustainable yield (MSY), to account for the ecological services delivered by commercial species, and we show that a more holistic and conservative approach to maintain ecosystem functioning, where ecological dynamics can manifest alternative community states and where phase shifts are difficult to reverse, is essential for the long term sustainability of the fishery.

Chapter 2 Exploring alternative states in ecological systems with a qualitative analysis of community feedback

2.1 Abstract

Demonstrating and predicting the existence of alternative states in natural communities remains a challenge for ecologists and is essential for resource managers. Positive feedback is often presented as central in maintaining alternative ecosystem states, but no formal approach relates this part of theory to real world applications. Through qualitative modelling of community response to long-term perturbations, we define generic mechanistic links between positive feedback and the occurrence of alternative states. Positive feedback diminishes a systems overall resistance to change, and can create and maintain correlations in the relative abundance of variables that coincide with alternative states. Through specific models of the dynamics of Tasmanian rocky reef communities, which are affected by climate and fishing and persist within alternative states, we demonstrate the ability of our theoretical framework to predict alternative states in ecosystems and inform management intervention. A qualitative knowledge of community structure permits a thorough analysis of system feedback and an assessment of the potential for an ecosystem to exhibit alternative states. We illustrate the usefulness of the approach to inform management priorities, and to focus monitoring and field research on the key drivers of ecosystem dynamics.

2.2 Introduction

Ecological communities can manifest phase shifts in which large changes in species abundances are observed without any tendency to return to the previous configuration (Scheffer et al., 2001). Alternative states have been reported both in terrestrial and aquatic systems (Schroder et al., 2005), with shifts from one state to another that can be smooth

or abrupt (Scheffer et al., 2001; Beisner et al., 2003). There has been a resurgence of interest in phase-shift theory over the last few decades (Petraitis and Dudgeon, 2004) as the effects of human activities on ecosystems become better understood (Scheffer et al., 2005; de Young et al., 2008; Ling et al., 2009*a*). Dramatic phase shifts, their potential anthropogenic genesis, and their associated effects on the livelihoods of those who rely on natural resources, have become a major concern for resource managers. Two main types of perturbations can alter the state of an ecosystem: 1) a sudden stochastic event that modifies state variables on short time scales (e.g. an extreme weather event that causes a dramatic mortality event for a population) and 2) a sustained external constraint (e.g. fishing pressure) that affects population growth rates (birth, mortality or migration) over long time scales (Scheffer et al., 2001; Beisner et al., 2003).

Evidence for alternative states in nature is often collated only after the dramatic consequences of a shift become evident (Scheffer et al., 2005; Ling et al., 2009*a*). While there exists a body of theoretical literature about alternative states and phase shifts, demonstrating their existence in natural systems (Petraitis and Dudgeon, 2004) and predicting their effects on ecosystem function remain as major challenges for ecologists and managers (de Young et al., 2008; Overland et al., 2008). While quantitative ecosystem models have a central role in helping to predict and understand alternative states, they remain difficult to parameterise and validate (Levins, 1998; Scheffer and Carpenter, 2003 but see Mumby et al., 2007 as a useful example). A central aspect of this problem is the relevance of positive feedback in creating and maintaining alternative states. Positive feedback has been recognised as a necessary but not sufficient condition for alternative states in both the theoretical literature (Thomas, 1981; Cinquin and Demongeot, 2002; Soulé, 2003) and the empirical ecological literature (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Nevertheless, while conceptual models have been used to illustrate phase shifts and positive feedback in ecosystems (Beisner et al., 2003; Suding et al., 2004), there remains a gap between theory and practice. Specifically, a formal mathematical approach based on the feedback properties of natural systems is lacking.

Around Tasmania in south-eastern Australia, subtidal rocky reefs typically occur in one of two alternative states (Fig. 2.1). In one state, the reef is dominated by a dense cover of seaweed (the seaweed bed state) but, where there is overgrazing of seaweeds by sea urchins, seaweed beds are denuded and reduced to bare rock (the sea urchin

barren state). Additionally, the understorey of intact seaweed beds can be dominated by alternative epilithic community types that can be described as either pink-benthos (dominated by encrusting algae) or brown-benthos (dominated by sessile invertebrates and a semi-consolidated matrix of filamentous algae and sediment) states. Tasmanian rocky reef communities offer a well-studied example of an ecological system with alternative states and this paper explores the general dynamics of these states and likely mechanisms that underlay their formation and maintenance.

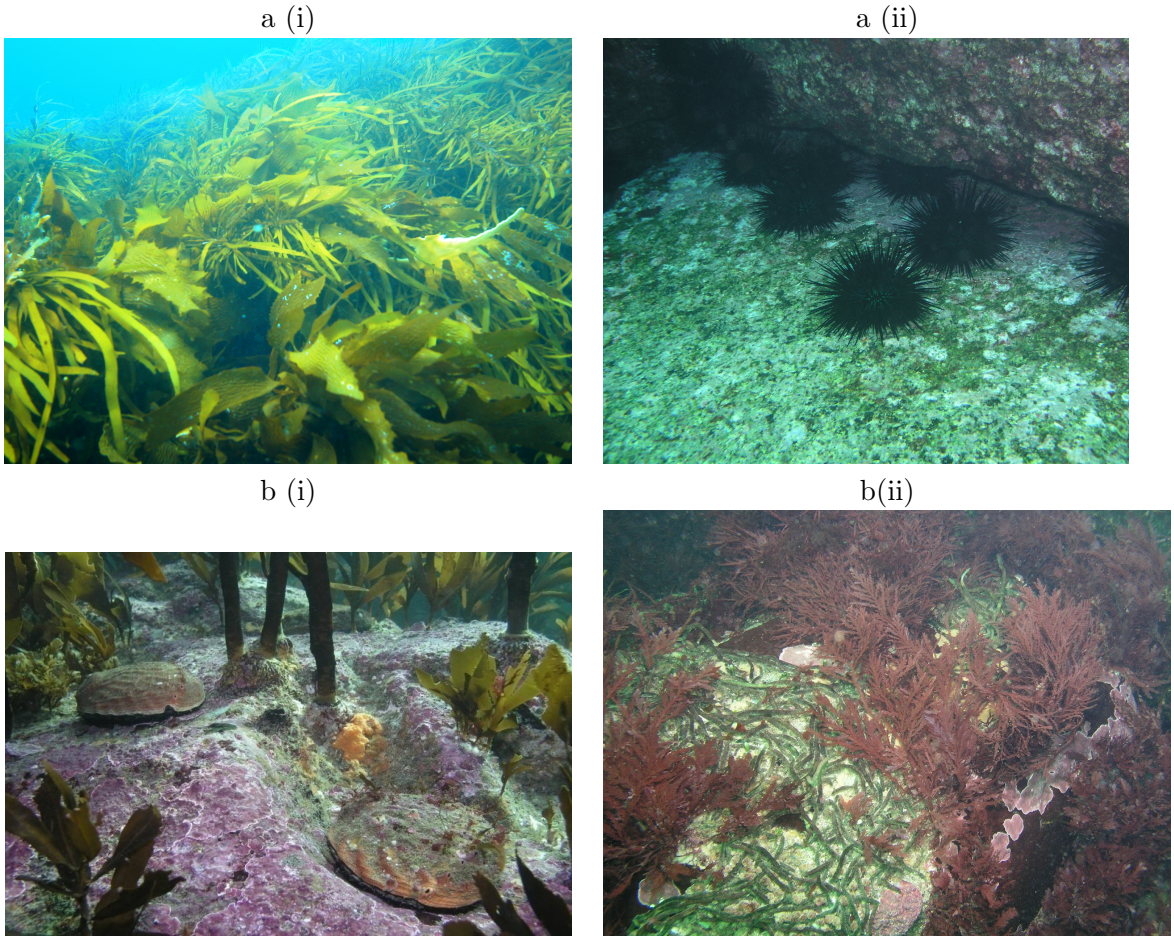


Figure 2.1: Examples of the alternative states observed on Tasmanian subtidal rocky reefs. a) (i) intact macroalgal canopy of *Ecklonia radiata* and *Phyllospora comosa*; a) (ii) barren habitat and long-spined sea urchin *Centrostephanus rodgersii*; b) (i) blacklip abalone *Haliotis rubra*, pink encrusting coralline algae, canopy of *Ecklonia radiata*; b) (ii) matrix of green algae, red filamentous algae and sediment. Photo credits: S.D. Ling; J.P. Valentine; C.R. Johnson.

Overstorey states: seaweed bed versus sea urchin barren (Fig. 2.1a).

Sea urchin barrens constitute an impoverished state compared to productive macroalgal beds (Ling, 2008), and are observed in many temperate regions around the globe (Lawrence, 1975; Mann, 1982; Chapman and Johnson, 1990; Steneck et al., 2004). Since the 1980s, sea urchin barrens up to 10-50 ha in extent have become established in exposed shallow-water regions on the northeast coast of Tasmania as a consequence of intensive grazing by the sea urchin *Centrostephanus rodgersii* (Johnson et al., 2005). This sea urchin has extended its range southward from New South Wales to the east coast of Tasmania as a result of enhanced dispersal of larvae from strengthened flow of the East Australian Current (Johnson et al., 2005; Ling et al., 2009*b*). Increase in the abundance of *C. rodgersii* and depletion of large lobsters (as a key predator of the sea urchin) by fishing have been identified as the two critical factors driving the shift to the barren state (Ling et al., 2009*a*). In Tasmania, high-value blacklip abalone (Haliotis rubra) and southern rock lobster (*Jasus edwardsii*) fisheries, with a combined value of about AUD$150M pa, decline on urchin barrens (Johnson et al., 2005).

Dominant understorey states: pink benthos versus brown benthos (Fig. 2.1b).

On subtidal reefs in eastern Tasmania, epilithic understorey assemblages under seaweed canopies are often dominated either by non-geniculate coralline algae and other encrusting algal species (the pink state), or by sessile invertebrates and filamentous red algae that capture and bind sediments to form a semi-consolidated matrix (the brown state). Brown benthos is generally avoided by emergent abalone and ostensibly reduces settlement of abalone larvae and recruitment of abalone juveniles (Strain, 2009). Manipulative experiments indicate that the shift from pink to brown benthos states can be driven by heavy fishing of legal size abalone (Haliotis rubra) as a key herbivore in the system (Strain, 2009). Abalone grazing maintains pink encrusting algae by preventing their overgrowth by invertebrates and filamentous red algae. However, as the brown benthos establishes, abalone populations are locally reduced as they avoid this habitat type (Strain, 2009).

On Tasmanian rocky reefs, manipulative experiments have been carried out at small scales (e.g. 0.25x0.25m to 4x4m plots in Strain, 2009). While these studies help to refine understanding of the ecology of individual species (e.g. Ling et al., 2009*b*), and a

limited number of pairwise interactions (e.g. Strain, 2009), we lack the practical ability to carry out controlled experiments at a scale sufficiently large to understand how these species and interactions affect the dynamics of the larger system (Schroder et al., 2005). Given the lack of precise quantification of ecological processes, we adopt Puccia and Levins (1985) loop analysis (referred to as qualitative modelling in this paper) to develop a causal understanding of the qualitative dynamics of subtidal rocky reefs in eastern Tasmania. This method emphasises the contribution of the structural feedback properties of a system rather than the precise magnitude of its species interactions. We first identify generic and mechanistic links between positive feedback and occurrence of alternative states in ecosystem dynamics, and test this theoretical framework against specific examples from Tasmanian reef communities.

We develop models of Tasmanian reef systems where interactions were informed by both empirical observations and results of manipulative experiments (e.g. Johnson et al., 2005; Guest et al., 2009; Ling et al., 2009*a*; Strain, 2009). As our models focus on general community dynamics, they only explicitly represent individual key species (e.g. *C. rodgersii*, lobsters, abalone) and the species assemblages (e.g. seaweed bed) on which these species depend for food and habitat. As part of a larger study that includes quantitative models of subtidal rocky reef communities around Tasmania, we use qualitative modelling to 1) investigate the role of positive feedback in structuring the responses of natural systems to perturbations, 2) understand and predict the long-term ecosystem effects of perturbations from fishing rock lobster and abalone, and an increase in sea urchin abundance, and we confront model predictions with empirical results about system dynamics. 3) We also test the potential influence of uncertain ecological interactions and the importance of model structure to system dynamics (Dambacher et al., 2002). Through these models of Tasmanian reefs, we illustrate and discuss the ability of qualitative modelling to predict alternative states in ecosystems and inform management interventions.

2.3 Material and Methods

First, we provide a brief introduction to the methods of qualitative modelling through two generic three-variable ecosystem models (models 1 and 2; Fig. 2.2), and then analyse the influence of positive feedback on system dynamics using generic example models (Fig. 2.2

and 2.3). Finally, we present a suite of models of Tasmanian rocky reef communities as a case study to test the value of the approach to detect the potential for alternative states in ecological systems (Fig. 2.4-2.6).

2.3.1 Qualitative modelling of ecosystem feedback: generic models

A model can be represented as a signed directed graph (Fig. 2.2a and 2.3a), where variables, whether individual species or species assemblages (functional groups), are depicted graphically as nodes. Nodes are connected by links that represent the sign of direct effects (Puccia and Levins, 1985). Graphically, an arrow ($\rightarrow$) signifies a positive interaction (e.g. a prey contributes to a predators diet), a line with a filled circle ($-\circ$) represents a negative effect (e.g. depletion of a prey population by a predator). Self-effects are represented as lines originating and terminating at the same node (e.g. $\circlearrowleft$ for a positive self-effect).

Interacting populations can also be described through a set of Lotka-Volterra equations

$$\frac{d\mathbf{N}}{\mathbf{N}dt} = \mathbf{AN} + \mathbf{k} \tag{2.1}$$

where the rate of change in abundance of population variable $\mathbf{N}_i$ is controlled by rates of birth, death and migration. These rates can be embodied as interactions within and between populations (e.g. consumption-based birth or death rates), which are summarised in the community matrix $\mathbf{A}$, or effects that are intrinsic to the population (e.g. non-predation mortality), which are summarised in the vector $\mathbf{k}$. Each $a_{i,j}$ element of the community matrix represents the direct effect of variable j on variable i, and thus the sign structure of $\mathbf{A}$ is equivalent to the sign directed graph of the system (Fig. 2.2a; Fig. 2.2b). Thus for model 2, a positive direct effect of variable 2 on variable 3 is shown in the signed digraph as an arrow leading from node 2 to node 3, and in the community matrix as the positive term $a_{3,2}$.

In Eq. 2.1, the system of equations is at an equilibrium state when the rate of change for each population is zero, and the equilibrium abundances are denoted by an asterisk ($\mathbf{N^*}$). This equilibrium is maintained by the constancy of the rates in $\mathbf{A}$ and $\mathbf{k}$. For a change in

any system parameter (∂p_h), the shift in abundance for each population is calculated as

$$\frac{d\mathbf{N^*}}{dp_h} = -\mathbf{A}^{-1}\left[\frac{\partial \mathbf{A}}{\partial p_h}\mathbf{N^*} + \frac{\partial \mathbf{k}}{\partial p_h}\right] \tag{2.2}$$

While Eq. 2.2 can be used to predict changes in equilibria, it requires full quantification of the systems parameters. We can however approach this equation through a qualitative analysis considering only the sign structure of the community matrix (Dambacher et al., 2005). From the matrix equality: $-\mathbf{A}^{-1} = adj(-\mathbf{A})/det(-\mathbf{A})$, Eq. 2.2 can be rewritten as

$$d\mathbf{N^*} = \underbrace{\frac{-1}{(-1)^{n+1}det(\mathbf{A})}}_{\text{overall system feedback}} \underbrace{adj(-\mathbf{A})}_{\text{relative response}} \underbrace{\left[\frac{\partial \mathbf{A}}{\partial p_h}\mathbf{N^*} + \frac{\partial \mathbf{k}}{\partial p_h}\right] dp_h}_{\text{strength of input}} \tag{2.3}$$

where *det* is the matrix determinant, *adj* is the classical adjoint, or adjoint, matrix, and n is the number of variables or size of the system. The matrix determinant represents the systems resistance to a long-term perturbation and scales the magnitude of all of its responses, while the adjoint matrix details the relative response of each variable to a perturbation or input to a specific variable. In the first term of Eq. 2.3 we use a somewhat complicated multiplier for the system determinant, which maintains a sign convention for both even- and odd-sized systems. This is for two practical purposes. Firstly, we wish to consider that system stability depends on negative feedback being stronger than positive feedback, and the denominator of the first term of Eq. 2.3, which defines the overall system feedback, will be negative in any stable system. Secondly, it follows that for a stable system, the entire first term of Eq. 2.3 will be positive (Dambacher et al., 2003), and thus the adjoint matrix will return the correct sign for a positive input to the system. Positive inputs arise from an increase in a rate of birth or immigration or a decrease in a rate of death or emigration, while negative inputs come from the opposite processes (e.g. increased rate of death, etc.).

In a qualitative analysis we are interested only in the sign of the input rather than its magnitude, and thus we can omit the last term of Eq. 2.3 and use the sign (*sgn*) of the adjoint matrix to predict the direction of change in population abundances

$$sgn(\triangle \mathbf{N^*}) = sgn(adj(-\mathbf{A})). \tag{2.4}$$

Eq. 2.4 returns the qualitative change in equilibrium abundance for the system due to

positive inputs in the abundance of a variable; for negative inputs the signs of the adjoint matrix are simply reversed. For a more detailed derivation of the above equations, see Dambacher et al. (2005). In Fig. 2.2, adjoint matrices for models 1 and 2 are given in symbolic and qualitative form. Inputs are read down the column of the input variable, and responses along the rows. For example, a positive input to variable 1 is read down the first column, and for both models 1 and 2, the predicted response of variable 2 to this input is a decrease in abundance: this is read as the first element of the second row, which is detailed as -$a_{2,1}a_{3,3}$ in the symbolic adjoint matrix (Fig. 2.2c) and a negative sign in the qualitative adjoint matrix (Fig. 2.2d). For a negative input, the sign of this response would be switched to positive.

For the models presented later in this paper, we use qualitative adjoint matrices where variable responses can be completely determined when all terms in an element of the symbolic adjoint matrix are of the same sign. When both negative and positive terms occur, however, the predicted sign of the response is ambiguous, and the sign of the predicted response depends on the relative strength of specific interactions. For example, in model 2, the predicted response of variable 1 to an input to variable 2 has both positive ($a_{1,2}a_{3,3}$) and negative (-$a_{1,3}a_{3,2}$) terms (Fig. 2.2c). In this instance, if the relative strength of the terms were known, then a qualitative prediction could be made based on an algebraic condition. Thus, if the direct effect of variable 3 on 1 was known to be relatively strong, then it is likely that condition 1 ($a_{1,2}a_{3,3} < a_{1,3}a_{3,2}$) is true, and variable 1s response would be negative. In this study, ambiguous predictions are given in brackets within the qualitative adjoint matrices, and the algebraic conditions supporting the predicted signs are denoted as superscripts (e.g. Fig. 2.2d). When no simple interpretation or assumption can elucidate ambiguity, the qualitative prediction is given as a question mark.

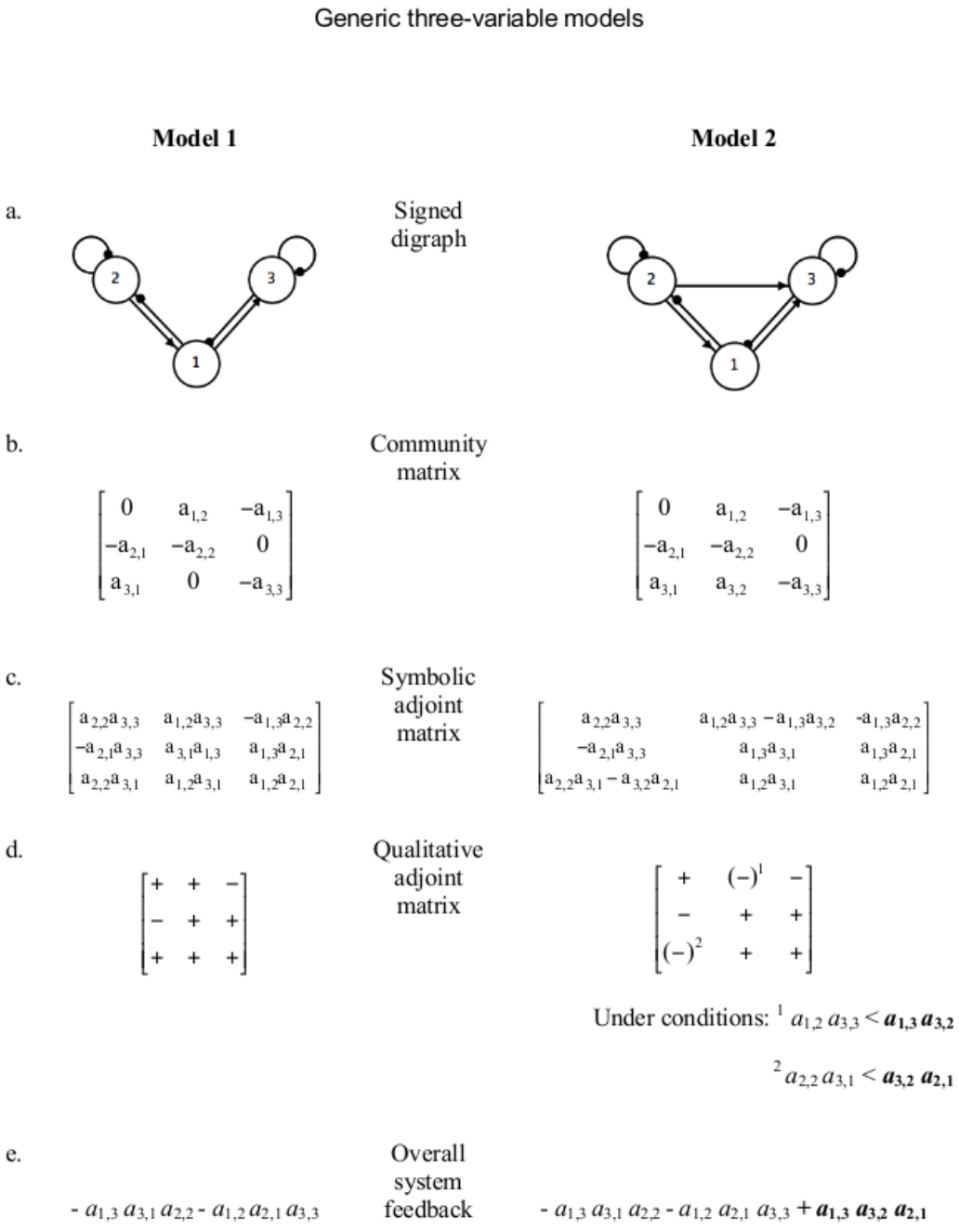


Figure 2.2: Models 1 and 2 are generic three-variable models. Each qualitative model is given as (a) a sign-directed graph associated with (b) a symbolic community matrix ($\mathbf{A}$), and adjoint matrices of the negative of the community matrix given in (c) symbolic ($adj(-\mathbf{A})$) and, in (d) qualitative form ($sgn(adj(-\mathbf{A}))$). The numbers given in the nodes of the graph define the positions of each variable in the matrices. In the qualitative adjoint matrix, ambiguous predictions are given in parentheses with the condition supporting the predicted sign in superscript (e.g. $(+)^i$ for a positive response under condition i). The determinant of the community matrix, or overall system feedback ($det(\mathbf{A})$), is given symbolically with the positive feedback cycles highlighted in bold (e).

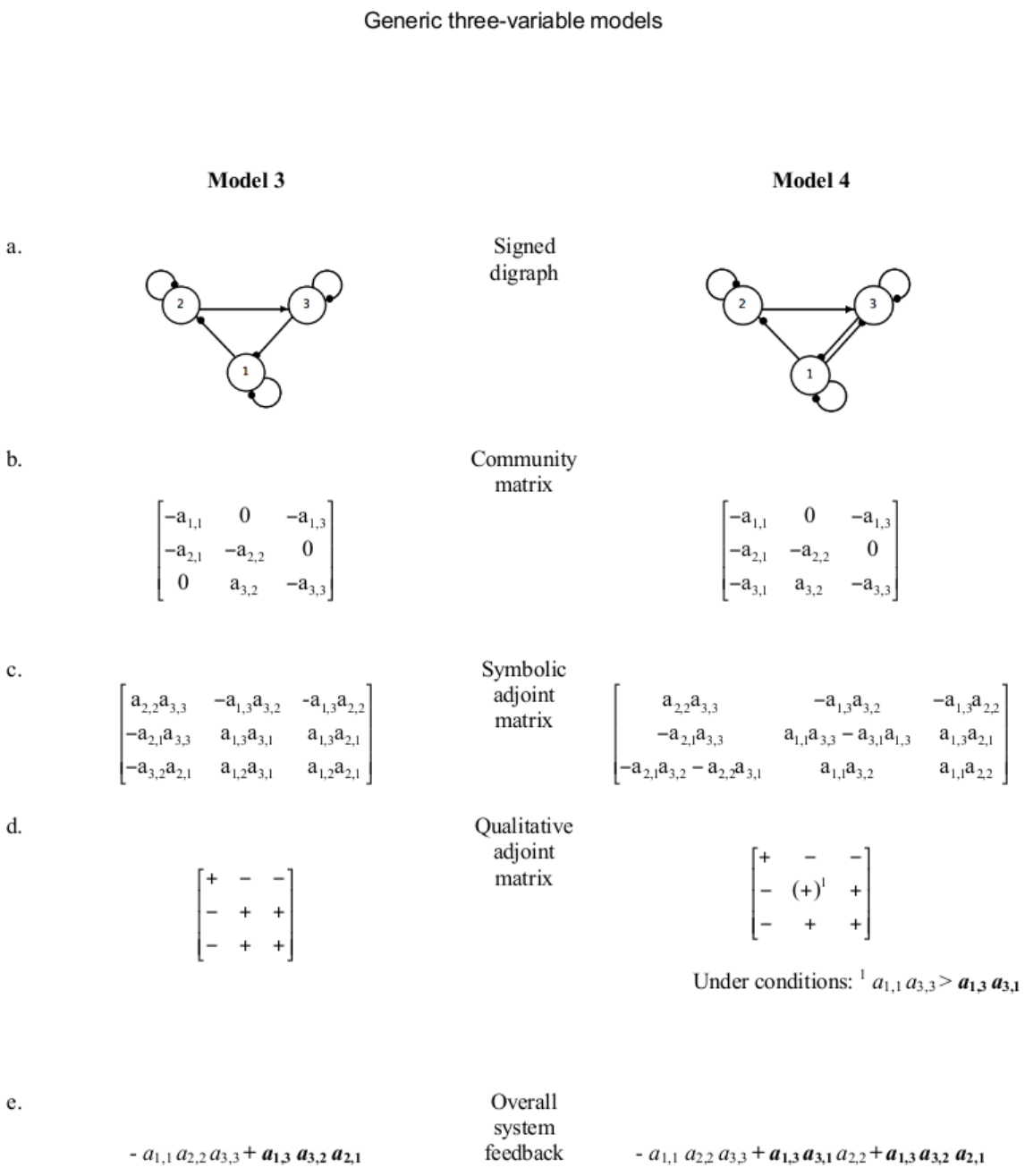


Figure 2.3: Models 3 and 4 are generic three-variable models. Each qualitative model is given as (a) a sign-directed graph associated with (b) a symbolic community matrix ($\mathbf{A}$), and adjoint matrices of the negative of the community matrix given in (c) symbolic ($adj(-\mathbf{A})$) and, in (d) qualitative form ($sgn(adj(-\mathbf{A}))$). The numbers given in the nodes of the graph define the positions of each variable in the matrices. In the qualitative adjoint matrix, ambiguous predictions are given in parentheses with the condition supporting the predicted sign in superscript (e.g. $(+)^i$ for a positive response under condition i). The determinant of the community matrix or overall system feedback ($det(\mathbf{A})$), is given symbolically with the positive feedback cycles highlighted in bold (e).

2.3.2 Role of positive feedback in creating alternative states

While negative feedback is a process (e.g. prey-predator relationships) that brings a variable back towards its original value in response to a perturbation, positive feedback (e.g. competition between two species) gives rise to a chain of events that keeps displacing a variable away from its original value in the same direction as the initial change (Levins, 1998). Positive feedback structures how a system will respond to a perturbation in two important ways through its influence on both the first and second term of Eq. 2.3. In the first term, positive feedback can weaken the overall system feedback, thereby increasing the sensitivity of the system to a given perturbation. In the second term, positive feedback affects the relative magnitude and sign of each variables response, as detailed in the elements of the systems adjoint matrix. The importance of these two influences is next explored through a number of example model systems (Fig. 2.2 and 2.3).

(i) Positive feedback weakens system resistance to a perturbation. The overall feedback of a system can be made up of both positive and negative feedback cycles, and even where the net feedback is negative, the presence of positive cycles will increase a systems sensitivity to a perturbation. For instance, model 2 only differs from model 1 by the presence of a positive link from variable 2 to 3 and, compared to model 1, its overall feedback is diminished by the presence of a single positive feedback cycle $a_{1,3}a_{3,2}a_{2,1}$ (Fig. 2.2e), which decreases its resistance to a perturbation. For an input to variable 3, the algebraic arguments in the third column of the adjoint matrices are identical for both models 1 and 2 (Fig. 2.2c), but by virtue of the $a_{3,2}$ link, which does not even enter into the algebraic arguments in the third column of model 2's adjoint, the magnitude of model 2's responses will be greater.

(ii) Positive feedback can structure alternative states. The elements of a systems adjoint matrix can provide a mechanistic understanding of how each variables response will be influenced by the feedback properties of the perturbed system. In general, the elements of the adjoint matrix are composed of subsets of the feedback cycles detailed in the system determinant. Thus, where the effect of positive feedback is strong, then its effect can be traced through individual response predictions in the adjoint matrix. In systems with strong positive feedback, correlations in the predicted changes in equilibrium values can emerge in the adjoint matrix that are consistent with alternative states.

Models 1 and 3 provide a sharp contrast for the effects of positive and negative feedback on correlation patterns in the adjoint matrix. Model 3 (Fig. 2.3) is an example of a system where only positive feedback emerges from interspecific links. The rows of the adjoint matrix for this system show a perfect pattern of correlation: variables 2 and 3 are always positively correlated with each other and negatively correlated with the predicted responses of variable 1. Thus, this model demonstrates a potential to maintain two alternative states where either variables 2 and 3 are at a relatively high abundance and variable 1 is at a relatively low abundance, or *vice versa*. In model 1, which lacks any positive feedback, the rows of the adjoint matrix do not show a regular pattern of correlation. For instance, the responses of variables 1 and 2 are negatively correlated to an input to variable 1, but positively correlated when the input is via variable 2.

In natural systems, the influence of positive feedback on community responses is hardly ever as clearly evident as in model 3, as system dynamics are usually determined by a mix of both positive and negative feedback cycles. Models 2 and 4 (Fig. 2.2 and 2.3) contain both positive and negative feedback cycles that create ambiguous response predictions, and potentially inconsistent correlation patterns in the adjoint matrix. These ambiguities, however, can be interpreted to understand how the relative strength of positive and negative feedbacks can contribute to alternative states.

In model 2 the right-hand side of the condition 1 and 2 (Fig. 2.2d) are subsets of the positive feedback cycle detailed in the determinant for each model system (Fig. 2.2d and e). Thus, if the interactions creating the positive feedback ($a_{2,1}$, $a_{1,3}$, $a_{3,2}$) are sufficiently strong then conditions 1 and 2 are likely to prevail, in which case the rows of the qualitative adjoint matrix (Fig. 2.2d) will show regular correlations, and the system can maintain two alternative states. In model 4, condition 1 ($a_{1,1}a_{3,3} > a_{1,3}a_{3,1}$) is guaranteed by system stability, which requires the overall system feedback to be negative (i.e. $a_{1,1}a_{2,2}a_{3,3} > a_{1,3}a_{3,1}a_{2,2}+a_{1,3}a_{3,2}a_{2,1}$). Hence, under the assumption of system stability, the qualitative adjoint matrix of model 4 is consistent with two alternative states (Fig. 2.3).

This example illustrates how the presence of positive feedback cycles can structure correlations in variables equilibrium values, and can contribute to the occurrence of alternative states. For models 2-4, an input to any variable in the system has the potential to either reinforce the existing state or shift the system to the alternative state. Model 1,

however, lacks positive feedback and thus does not have a system structure that supports the existence of alternative states. In models 2 and 4, ambiguous predictions can be interpreted assuming conditions of 1) relatively strong positive feedback (model 2), or 2) system stability (model 4), so that regular correlation patterns consistent with alternative states emerge in the adjoint matrix. A simple but important feature demonstrated in models 3 and 4 is whether or not a positive feedback cycle contains an even number of negative links or just positive links. Where positive feedback has an even number of negative links (Models 2 and 4; Fig. 2.2) then alternative states will be characterized by both positive and negative correlations among variables, where there is only positive links then all variables will be positively correlated.

The absolute effect of positive feedback on the system determinant (i.e. diminished resistance to change) is difficult to quantify in practice. However, the occurrence of regular correlation patterns in the qualitative adjoint matrix constitute a reliable means to characterize the influence of positive feedback and the potential for alternative states in ecosystem dynamics. Next, we test the utility of this framework through models of Tasmanian rocky reefs, where communities persist within alternative states, and have been affected by a sustained fishing pressure and an increase in the abundance of sea urchins (Ling et al., 2009*a*).

2.3.3 Model specification

We collated empirical data on the different components of subtidal rocky reefs in Tasmania, identifying key variables and interactions between them (Table 2.1). Our models address general community dynamics and only represent key species, and the essential species assemblages in terms of food or habitat support for these species; abalone (AB), southern rock lobster (RL) and long-spined sea urchins (CR for *Centrostephanus rodgersii*) are considered as individual species. Seaweed bed (SW) includes canopy-forming algae such as *Ecklonia radiata*, *Macrocystis pyrifera*, *Phyllospora comosa* and a raft of other fucoid macroalgae comprising numerous understorey seaweeds as well as associated assemblages of invertebrates. Thus, SW represents an essential source of food and habitat for abalone, rock lobster and the sea urchins. Basal-level benthic communities are described as either pink benthos (PB, i.e. pink encrusting algae comprising non-calcareous encrusting and calcareous non-geniculate coralline algae) or brown benthos (BB, i.e. sessile invertebrates

and a matrix of filamentous red algae and sediment). Each variable is self-regulated to account for density-dependent processes and an external supply of recruits (Puccia and Levins, 1985).

A wide range of environmental conditions and fishing pressure affects temperate reefs along the east coast of Tasmania. Rather than considering a single model including every possible interaction, we break our analysis into sets of different models to capture the variability in community structure between regions. This array of models does not address the magnitude of variability encountered in the community composition of each state, rather it summarises the alternative configurations observed on Tasmanian reefs as they relate to general functioning and provision of ecosystem services. These models are meant to account for the range in productivity, habitat structure and state of the commercial fisheries within rocky reef communities at a scale ranging from 10 m^2 to 10 ha. Based upon available knowledge, we assessed the strength or certainty of each models ecological interactions (Table 2.1) to tackle model structure uncertainty.

Table 2.1: Ecological interactions represented in our models of Tasmanian rocky reef communities. Interaction strength is explicitly described to identify the links to be tested in the models. SW: seaweed bed including canopy-forming macroalgae; CR: long-spined sea urchin, *Centrostephanus rodgersii*; RL: southern rock lobster, *Jasus edwardsii*; AB: blacklip abalone, *Haliotis rubra*; BB: brown benthos, understorey of sessile invertebrates and a matrix of filamentous algae and sediments; PB: pink benthos, i.e. non-calcareous encrusting algae and non-geniculate coralline algae.

Interaction	Description	Strength	References
Strong interactions that constitute the basis of the overstorey models (A to D)			
SW →RL	Provision of habitat and food	Strong	(Guest et al., 2009)
SW →AB	Provision of habitat and food (drift materials)	Strong	(Guest et al., 2008)
SW →CR	Source of food	Strong	(Ling, 2008)
RL —∘ CR	Predation by large rock lobster (carapace length > 140mm)	Strong	(Ling et al., 2009*a*)
CR —∘ SW	Grazing	Strong	(Ling, 2008)
Variable interactions, which inclusion is tested in the overstorey models			
RL—∘ AB	Predation on juveniles; Reduction of abalone access to food	Moderate	(Pederson et al., 2008)
CR —∘ AB	Competition for space and resource	Moderate	(Strain, 2009)
Constant interactions that constitute the basis of the understorey models (E to G)			
SW →PB	Provision of optimal light conditions through shading	Strong	(Irving et al., 2004)
BB —∘ PB	Competition. Overgrowing of the pink algae	Strong	(Strain, 2009)
PB —∘ BB	Anti-fouling by sloughing of epithelial cells; allelochemicals	Weak	(Nylund and Pavia, 2005)
Variable interactions included in the models depending on the state of the understorey and site conditions (e.g. depth, exposure)			
PB →AB	Provision of habitat for adult and juvenile stages (pink state)	Variable	(Strain, 2009)
SW —∘ BB	Sweeping of young plant recruits (pink state, in exposed areas)	Variable	(Irving and Connell, 2006)
AB —∘ BB	Grazing and trampling / bulldozing (pink state)	Variable	(Strain, 2009)
BB —∘ SW	Blocking macroalgae recruitment (brown state with sediments, in sheltered areas)	Variable	(Valentine and Johnson, 2005)
BB —∘ AB	Hostile habitat for adult and recruits (brown state)	Variable	(Strain, 2009)

Overstorey models.

The alternative overstorey models (Fig. 2.4a) capture the known range of possible effects of grazing by the sea urchin *Centrostephanus rodgersii* on the seaweed canopy and the main commercial invertebrate reef species. A macroalgal-dominated overstorey versus sea urchin barrens constitute the two alternative states of the overstorey community, and are characterised by the presence or absence of a dense seaweed canopy (Fig. 2.1a). Large lobsters (carapace length >140 mm), which are harvested by fishing, are the main natural predators of the invasive sea urchin (Ling et al., 2009*a*). However, lobsters are generalist feeders and the sea urchin does not constitute the core of their diet (Guest et al., 2009). Thus, other connections are also possible. The suite of models A to D (Fig. 2.4a) tests the effects of including these uncertain interactions ('RL—∘AB' and 'CR—∘AB'; see Table 2.1) on overstorey dynamics. We discuss model predictions against empirical field observations of the qualitative effects of a positive input in the abundance of *C. rodgersii* (CR) or rock lobster (RL) on other overstorey variables (Fig. 2.4b).

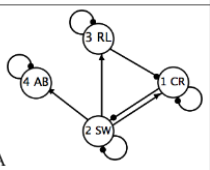
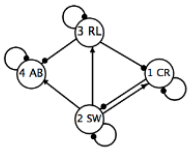
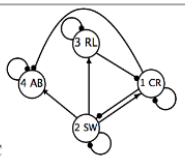
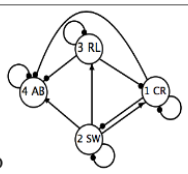
Understorey models.

The alternative models of the understorey (Fig. 2.5a) address key changes in dominant interactions within each state of the benthic community under the macroalgal canopy. As either the pink- or the brown-benthos dominated state (Fig. 2.1b) establishes, the abundances of understorey variables vary significantly (Strain, 2009; Strain and Johnson, 2012), which affects the strength of some interactions (Table 2.1) hence community structure. Model E (Fig. 2.5a) considers every possible interaction, while models F and G (Fig. 2.5a) only include the dominant interactions in each of the pink- and the brown-benthos dominated states, respectively. The pink-benthos state, dominated by encrusting algae, is sheltered from direct sunlight by the dense seaweed canopy and is maintained clean from invertebrates and recruiting filamentous algae by the grazing (and perhaps 'bulldozing') effects of abalone (model F; Fig. 2.5a). Reciprocally, the pink coralline algae constitute an essential habitat for adult abalone, the metamorphosis of larvae and development of juveniles. However, as the brown benthos overgrows the encrusting algae (model G; Fig. 2.5a), abalone begin to avoid the overgrowth areas (Strain and Johnson, 2012), causing abalone to no longer significantly impact on other variables. In more sheltered areas, along with the proliferation of sessile invertebrates, red filamentous algae

act to bind sediments and form a semi-consolidated sediment matrix, which inhibits the recruitment of native canopy-forming macroalgae (Valentine and Johnson, 2005). We confront understorey model predictions with observed effects of an input in the abundance of brown benthos, abalone, or the seaweed bed (Fig. 2.5b).

Overstorey models

a)

Sign-directed graph	Interactions included	Adjoint(-A)
 A	• Strong interactions	Positive input to CR SW RL AB CR [+ (–)[1] – 0] SW [– + + 0] RL [– + + 0] AB [– + + (+)[2]]
 B	• Strong interactions • RL → AB	Positive input to CR SW RL AB CR [+ (–)[1] – 0] SW [– + + 0] RL [– + + 0] AB [? ? ? (+)[2]]
 C	• Strong interactions • CR → AB	Positive input to CR SW RL AB CR [+ (–)[1] – 0] SW [– + + 0] RL [– + + 0] AB [– ? + (+)[2]]
 D	• Strong interactions • RL → AB • CR → AB	Positive input to CR SW RL AB CR [+ (–)[1] – 0] SW [– + + 0] RL [– + + 0] AB [? ? ? (+)[2]]

Under conditions:

1: $a_{1,3}\, a_{3,2} > a_{1,2}\, a_{3,3}$

2: $a_{1,1}\, a_{2,2}\, a_{3,3} + a_{1,2}\, a_{2,1}\, a_{3,3} > a_{1,3}\, a_{3,2}\, a_{2,1}$

Overstorey models

b)

Positive input to:

	CR	RL
CR	$+^{a}$	$-^{b}$
SW	$-^{a}$	$+^{b}$
RL	$-^{a}$	$+^{b}$
AB	$-^{a}$	$+^{b}$

[a] observations from both large-scale surveys of sea urchin barrens on the East coast of Tasmania (Johnson et al. 2005) and small-scale observations and experiments (Ling 2008; Strain 2009)

[b] monitoring of Tasmanian marine reserves (Barrett et al. 2009)

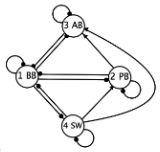
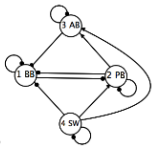
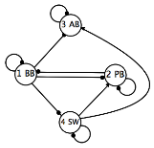
Figure 2.4: a) Models A to D of the overstorey dynamics. A signed-directed graph, a list of the interactions included and the qualitative adjoint matrix are provided for each model. SW stands for seaweed bed, RL for rock lobster, AB for abalone and CR for *Centrostephanus rodgersii*, the long-spined sea urchin. The numbers given in the node define the positions of each variable in the matrices. When an ambiguous prediction can be elucidated with simple assumptions, the sign is given between parentheses with a supporting condition referenced by a superscript number. These conditions are provided below the set of models. Question marks represent ambiguous predictions, where quantitative knowledge about the relative strength of some specific interactions is required to determine the sign of the response. b) Matrix presenting the observed effects of a positive to CR and RL on overstorey variables. The subscripts point to the supporting field observations that are specified below the matrix.

Model combining overstorey and understorey dynamics: example of the Maria Island marine reserve.

To illustrate the interdependencies between over- and understorey communities, model H (Fig. 2.6) combines the overstorey model B and the understorey model F as a representation of the dynamics in the Maria Island marine reserve on the east coast of Tasmania. The structure of model H is supported by field observations and experiments within the reserve. Over 20 years, protection from fishing at Maria Island has restored the pristine community state with a large biomass of large lobsters that maintains low densities of sea urchins though predation. The presence of large rock lobsters also negatively affects abalone directly through predation and indirectly by causing a greater proportion of animals to remain cryptic within the interstices of the reef (Pederson et al., 2008). The understorey community tends to be dominated by a pink benthos of encrusting algae, which is maintained by a relatively high abundance of abalone and, in shallow water, by the sweeping action of canopy-forming macroalgae on the substratum. Note that model H only captures the overall dynamics of an intact seaweed bed community, while many other combinations of understorey and overstorey models could adequately describe other configurations of Tasmanian reefs.

Understorey models

a)

Sign-directed graph	Interactions included	Adjoint(-A)
E 	• Constant interactions • Interactions associated with the 'pink' state: ○ SW ⟶ BB ○ AB ⟶ BB • Interactions associated with the 'brown' state: ○ BB ⟶ SW ○ BB ⟶ AB	Positive input to BB PB AB SW BB [+ − − −] PB [− (+)[1] + (+)[4]] AB [− (+)[2] (+)[3] (+)[5]] SW [− + + (+)[6]]
F 	• Constant interactions • Interactions associated with the 'pink' state: ○ SW ⟶ BB ○ AB ⟶ BB ○ PB → AB	Positive input to BB PB AB SW BB [+ − − −] PB [− + + +] AB [− + (+)[7] (+)[8]] SW [0 0 0 (+)[9]]
G 	• Constant interactions • Interactions associated with the 'brown' state: ○ PB ⟶ SW ○ PB ⟶ AB	Positive input to BB PB AB SW BB [+ − 0 −] PB [− + 0 +] AB [− + (+)[10] (+)[11]] SW [− + 0 (+)[12]]

Under conditions:

1: $a_{1,1}a_{3,3}a_{4,4} > a_{1,3}a_{3,1}a_{4,4} + a_{4,1}a_{1,3}a_{3,4} + a_{1,4}a_{4,1}a_{3,3}$

2: $a_{3,2}a_{1,1}a_{4,4} + a_{3,1}a_{1,2}a_{4,4} + a_{3,4}a_{4,1}a_{1,2} > a_{1,4}a_{4,1}a_{3,2}$

3: $a_{1,1}a_{2,2}a_{4,4} > a_{1,2}a_{2,1}a_{4,4} + a_{4,1}a_{1,2}a_{2,4} + a_{1,4}a_{4,1}a_{2,2}$

4: $a_{2,4}a_{1,1}a_{3,3} + a_{2,1}a_{1,3}a_{3,4} + a_{2,1}a_{1,4}a_{3,3} > a_{1,3}a_{3,1}a_{2,4}$

5: $a_{3,4}a_{1,1}a_{2,2} + a_{3,2}a_{2,4}a_{1,1} + a_{3,2}a_{2,1}a_{1,4} + a_{3,1}a_{1,2}a_{2,4} + a_{3,1}a_{1,4}a_{2,2} > a_{1,2}a_{2,1}a_{3,4}$

6: $a_{1,1}a_{2,2}a_{3,3} > a_{1,2}a_{2,1}a_{3,3} + a_{3,2}a_{2,1}a_{1,3} + a_{1,3}a_{3,1}a_{2,2}$

7: $a_{1,1}a_{2,2}a_{4,4} > a_{1,2}a_{2,1}a_{4,4}$

8: $a_{3,4}a_{1,1}a_{2,2} + a_{3,2}a_{2,4}a_{1,1} + a_{3,2}a_{2,1}a_{1,4} > a_{1,2}a_{2,1}a_{3,4}$

9: $a_{1,1}a_{2,2}a_{3,3} > a_{1,2}a_{2,1}a_{3,3} + a_{2,1}a_{1,3}a_{3,2}$

10: $a_{1,1}a_{2,2}a_{4,4} > a_{1,2}a_{2,1}a_{4,4} + a_{4,1}a_{1,2}a_{2,4}$

11: $a_{3,4}a_{1,1}a_{2,2} + a_{3,1}a_{1,2}a_{2,4} > a_{1,2}a_{2,1}a_{3,4}$

12: $a_{1,1}a_{2,2}a_{3,3} > a_{1,2}a_{2,1}a_{3,3}$

b)

Positive input to

	BB	AB	SW
BB	$+^{a}$	$-^{b}$	$-^{c}$
PB	$-^{a}$	$+^{b}$	$+^{d}$
AB	$-^{a}$	$+^{b}$	$+^{e}$
SW	?	?	$+^{d}$

[a] small-scale surveys; transplantation of abalone into the brown benthos (Strain 2009)

[b] abalone removal experiments (Strain 2009)

[c] field observations in shallow exposed area (see Irving and Connell 2006)

[d] canopy removal experiments (Irving et al. 2004)

[e] large-scale surveys of sea urchin barrens on the East coast of Tasmania (Johnson et al. 2005)

Figure 2.5: a) Models E to G of the understorey dynamics. A signed-directed graph, a list of the interactions included and the qualitative adjoint matrix are provided for each model. The numbers given in the nodes of the graphs define the positions of each variable in the matrices. BB stands for brown benthos, PB for pink benthos dominated by encrusting algae, AB for abalone and SW for seaweed bed. When a prediction is ambiguous, the sign is given in parentheses with a supporting condition referenced by a superscript number. All these conditions are provided below the models. b) Matrix presenting the observed qualitative effects of a positive input to BB, AB or SW on the understorey community. The subscripts point to the supporting field observations that are specified below the matrix.

2.4 Results

For all models, qualitative adjoint matrices (Fig. 2.4a, 2.5a and 2.6a) provide a comprehensive description of community responses to perturbation. When possible, ambiguous predictions are elucidated in the qualitative adjoint matrices under simple assumptions of strong positive feedback (e.g. condition 2; Fig. 2.6) or system stability (condition 2; Fig. 2.4a). The algebraic conditions that support the predicted signs are listed after each set of models (Fig. 2.4, 2.5 and 2.6). As model complexity increases with the number of interactions included, so does ambiguity. Question marks in the adjoint matrices indicate predictions where ambiguity remains and can only be interpreted with quantitative information about the relative strength of individual interactions.

2.4.1 Positive feedback and model dynamics

Overstorey models.

In all overstorey models (Fig. 2.4a), the positive feedback cycle 'SW→RL—∘CR—∘SW' ensures regular correlations among responses of SW, RL and CR. These correlations are contingent on strong positive feedback (condition 1) and model stability (condition 2). All adjoint matrices contain a block with similar sign predictions for the first 3 variables, i.e. responses to perturbations of the seaweed bed (SW) and rock lobster (RL) are always positively correlated, but negatively correlated with responses of *C. rodgersii* (CR). For instance, in the adjoint matrix of model A, a positive input to the abundance of CR (first column) positively affects CR (first row) and is detrimental to SW, RL and AB (respectively, second, third and fourth row). Positive inputs to the abundance of SW and RL (respectively, second and third row) induce the opposite effects, i.e. a decrease in CR abundance and an increase in SW, RL and AB.

While correlation patterns between SW, RL and CR hold in all adjoint matrices for models B to D (Fig. 2.4a), abalone (AB) do not necessarily respond in phase because they are not directly involved in the positive feedback and do not transmit feedback to any other variable. In model A, abalone dynamics are only under the influence of SW via the link $a_{4,2}$, hence AB reacts in phase with SW and RL. In models B to D (Fig. 2.4a), the additional links $a_{3,2}$ ('RL—∘AB') and $a_{3,4}$ ('CR—∘AB') exert opposing effects to $a_{3,1}$

('SW→AB') on abalone dynamics. Thus, the sign of the responses of abalone depends on the relative strength of these interactions and may or may not be in phase with the alternative states. When the barren state fully develops, abalone populations always respond negatively as the negative effect on abalone of the loss of the seaweed canopy greatly exceeds the magnitude of the combined negative effects on abalone of predation or threat of predation by rock lobster and competition with *C. rodgersii*. Thus, for all overstorey models (Fig. 2.4a), predictions of the qualitative effects of an increase in urchin abundance agree with empirical observations (Fig. 2.4b).

Understorey models.

In the understorey models (Fig. 2.5a), brown benthos (BB) always responds to changes in the direction opposite to abalone (AB), pink benthos (PB) and the seaweed canopy (SW). The correlation patterns in the adjoint matrices of models E and F concur with empirical observations of a brown- or pink-benthos dominated state. These correlations are caused by a number of positive feedback cycles (e.g. 'BB—∘PB—∘BB' in all models; 'AB—∘BB—∘PB→AB' in model E and F; 'BB—∘SW→PB—∘BB' in model E and G), and are also consistent across the ambiguous predictions, the signs of which were determined by conditions for system stability (i.e. conditions 1-12; Fig. 2.5a).

The correlation patterns consistent with alternative states hold in all adjoint matrices of the understorey models, despite differences in system structure. In the pink-benthos dominated state (model F; Fig. 2.5a), the positive feedback cycle 'AB—∘BB—∘PB→AB' dominates. Both abalone and the seaweed canopy, which remains unaffected by the other variables, contribute to the maintenance of the pink coralline algae. Conversely, once the brown-benthos dominated state is established (model G; Fig. 2.5a), the positive feedback cycle 'BB—∘SW→PB—∘BB' replaces the former one as the dominating driver of the dynamics and can directly affect the canopy cover by blocking macroalgae recruitment, while abalone no longer contributes strongly to feedback to any of the other variables. Understorey model predictions agree with known community effects of inputs to BB, AB or SW (Fig. 2.5b).

Model combining overstorey and understorey dynamics.

The adjoint matrix for model G coupling overstorey and understorey dynamics (Fig. 2.6) presents correlation patterns consistent with the alternative states observed when each

of the overstorey and understorey communities were considered separately. Conditions 1, 3 and 4 are related to the stability of each subsystem, while condition 2 assumes strong positive feedback (Fig. 2.6). Perturbations to the overstorey dynamics affect the understorey community through the effects of SW and RL on understorey variables. However, alternative states are not necessarily in phase between the two subsystems, as it is only the overstorey variables that transmit feedback to the understorey dynamic, and the effects of $a_{4,1}$, $a_{4,2}$, $a_{5,1}$ and $a_{6,1}$ exert opposing influences on understorey variables, the sign predictions of which are ambiguous.

2.4.2 Sustained perturbations and ecosystem states

Overstorey models.

In the adjoint matrices associated with model A to D (Fig. 2.4a), the qualitative effects of fishing rock lobster or abalone can be treated as a negative input to variables 3 or 4, and read as the negative of the 3^{rd} and 4^{th} columns of the adjoint matrix, respectively. An increase in sea urchin recruitment translates as a positive input to sea urchins, the effects of which are given in the 1^{st} column. For example, in model A, increasing fishing pressure on rock lobster results in a decrease in seaweed, rock lobster and abalone, and an increase in urchin density. An increase in *C. rodgersii* abundance produces similar effects. Thus, fishing rock lobster or an increase in the sea urchin population can both displace the state of the overstorey community towards the urchin barren state and shift ecosystem functioning away from its productive seaweed bed state, which is consistent with field observations (Fig. 2.4b; Johnson et al., 2005; Ling, 2008). Note that only the structure of models B and D allow for positive inputs to rock lobster abundance to negatively affect the abundance of emergent abalone as observed in marine reserves around Tasmania, where populations of large lobsters have rebuilt following over a decade of protection from fishing (Fig. 2.4b; Barrett et al., 2009).

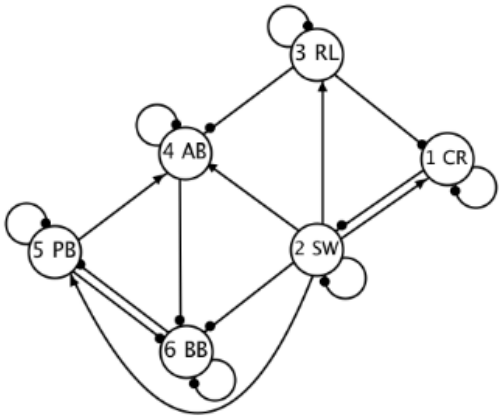
Understorey models.

While fishing abalone does not affect the overstorey community (Fig. 2.4a), it facilitates the establishment of the brown-benthos dominated state in the understorey models, where qualitative predictions of fishing abalone can be read as the negative of the 3^{rd} column

of the adjoint matrices (Fig. 2.5a). Accordingly to empirical observations (Fig. 2.5b; Strain and Johnson, 2010), harvesting abalone is predicted to weaken abalone services to the pink-benthos dominated state (models E and F) and can therefore facilitate a shift towards a brown-benthos dominated state in which ongoing fishing of abalone no longer affects community dynamics (model G). The change in qualitative predictions across the different models, where different positive-feedback mechanisms dominate in each state, illustrates the potential for a dramatic shift in the understorey dynamics under heavy abalone fishing.

Model combining overstorey and understorey in Maria Island marine reserve

a) Sign-directed graph



H

b) Adjoint(-A)

Positive input to

	CR	SW	RL	AB	PB	BB
CR	$(+)^1$	$(-)^{1\&2}$	$(-)^1$	0	0	0
SW	$(-)^1$	$(+)^1$	$(+)^1$	0	0	0
RL	$(-)^1$	$(+)^1$	$(+)^1$	0	0	0
AB	?	?	?	$(+)^{3\&4}$	$(+)^3$	$(-)^3$
PB	?	?	?	$(+)^3$	$(+)^3$	$(-)^3$
BB	?	?	?	$(-)^3$	$(-)^3$	$(+)^3$

Under conditions:

1: $a_{6,6}\, a_{5,5}\, a_{4,4} > a_{5,6}\, a_{6,5}\, a_{4,4} + a_{6,4}\, a_{4,5}\, a_{5,6}$

2: $a_{3,2}\, a_{1,3} > a_{1,2}\, a_{3,3}$

3: $a_{1,1}\, a_{2,2}\, a_{3,3} + a_{1,2}\, a_{2,1}\, a_{3,3} > a_{1,3}\, a_{3,2}\, a_{2,1}$

4: $a_{6,6}\, a_{5,5} > a_{6,5}\, a_{5,6}$

Figure 2.6: Model combining under- and overstorey dynamics of reef communities within the Maria Island marine reserve on the east coast of Tasmania. Signed-directed graph (a) and qualitative adjoint matrix (b) are provided. The numbers given in the node define the positions of each variable in the matrices. CR stands for *Centrostephanus rodgersii*, the long-spined sea urchin, SW for the seaweed bed, RL for rock lobster, AB for abalone, PB for pink benthos, and BB for brown benthos. When an ambiguous prediction can be elucidated with simple assumptions, the sign is given between parentheses with a supporting condition referenced by a superscript number. These conditions are provided below the set of models. Question marks represent ambiguous predictions, where quantitative knowledge about the relative strength of some specific interactions would be required to determine the sign of the response.

2.5 Discussion

In all models of Tasmanian rocky reefs, patterns in sign responses driven by the presence of positive feedback emerge in the adjoint matrices consistently with the alternative community states observed empirically. In overstorey systems, any perturbation, in particular lobster fishing or an increase in sea urchin abundance, pushes the community towards a dense seaweed bed supporting a high abundance of lobster or, alternatively, a sea-urchin-dominated barren with reduced seaweed cover and where lobster populations decline (Johnson et al., 2005; Ling et al., 2009*a*). In understorey systems, perturbations facilitate the establishment of either a brown- or a pink-benthos state, where abalone are typically lacking from the brown-state, and abundant in the pink-state (Strain and Johnson, 2010).

2.5.1 Ecosystem monitoring and management

Sets of variables or species that react in phase with alternative states present a particular interest for ecosystem monitoring and intervention. Correlations in sign predictions may rarely be consistent with alternative states for the whole model system, as ambiguous predictions increase throughout the qualitative adjoint matrix with increasing model complexity. As illustrated with abalone in the overstorey models, variables that are indirectly influenced by the positive feedback can respond with ambiguity and are not necessarily in phase with the alternative states. Still, a thorough analysis of the qualitative adjoint matrix of a system can help detect regular correlations, by either studying only the effects of a subset of long-term perturbations (i.e. selection of columns), or a subset of all the responses of modelled variables (i.e. selected rows). For example, Dambacher and Ramos-Jiliberto (2007) developed qualitative models of Danish shallow lakes, where the predicted responses of four of the ten model variables (in the adjoint matrix) displayed regular correlations with the alternative states of the lake system (either a clear-water or a turbid state). When such regular patterns emerge in the relative responses of some variables to sustained perturbation, qualitative modelling can guide the choice of the most appropriate set of indicators to monitor the evolution of ecosystem state. For instance, in the Tasmanian example, on the basis of the regular correlation identified in the overstorey models, a decrease in catch rates of rock lobster may constitute a reliable indicator of a deteriorating state of the seaweed bed towards a sea urchin barren. Even if other factors

(e.g. fishing, low recruitment) directly drive a decline in large lobsters, the model clearly identifies an increased risk of the system moving towards a sea urchin barren. Conversely, inconsistent predictions across overstorey models A to D discount abalone abundance as a reliable variable for monitoring the state of the overstorey community.

Thus, qualitative modelling can help to identify the most appropriate variables to reliably track the state of any particular system and focus management on the key drivers of ecosystem dynamics, although each particular context would deserve further specific considerations. For instance, from model predictions, abalone does not appear as an effective lever for management interventions against the spread of sea urchin barrens.

2.5.2 Assessing the potential for alternative states

In all models, correlation patterns in variable responses emerge and concur with the theoretical framework for alternative states presented above (Fig. 2.2 and 2.3). However, qualitative modelling can only partially contribute to the identification of alternative states in nature, as only observations and manipulative experiments can unequivocally demonstrate the existence of persistent alternative states (Petraitis and Dudgeon, 1999). If the demonstration of dominant positive feedback in system dynamics constitutes an insufficient proof of alternative states (Scheffer et al., 2001), this framework can nevertheless inform the needs for a precautionary management approach and further manipulative experiments.

Moreover, the approach provides some informative conditions about the relative balance required between positive and negative feedback for a system to display alternative states. In these models of Tasmanian rocky reef communities, we only use two general assumptions to elucidate ambiguous predictions: 1) the interactions creating the positive feedback are assumed to be sufficiently strong to overwhelm interactions shared with negative feedback cycles (e.g. condition 1 in Fig. 2.4a); but 2) positive feedback cycles are not so strong as to compromise system stability as defined in Dambacher et al. (2003), i.e. at each level of feedback, negative feedback cycles dominate over positive ones (e.g. condition 2 in Fig. 2.4a), which is consistent with the systems persistence through time. In the combined model of the marine reserve (Fig. 2.6), condition 1 relies more specifically on the stability of the understorey subsystem, which a fortiori is consistent with the stability

of the whole model system. Thus, correlation patterns consistent with alternative states generally require that positive feedback cycles be sufficiently, but not overwhelmingly, strong relative to negative feedback cycles to allow for system stability.

These algebraic conditions for alternative states in community dynamics are consistent with the two rules proposed by Thomas (1981) to relate the structure of regulatory networks to their dynamical properties: 1) the presence of a positive feedback cycle or circuit is a necessary conditions for multiple stable states, while 2) a necessary condition for the existence of an attractive cycle is the presence of a negative circuit. Several theoretical studies on cellular differentiation and genetic networks have illustrated Thomas conjecture using a range of mathematical modelling approaches (e.g. Cinquin and Demongeot, 2002; Soulé, 2003). Here, the conditions for the relative balance of positive and negative feedback cycles in our models are consistent with Thomas conjecture, and moreover define the parameter space where system dynamics can display alternative states in response to long-term perturbations. These conditions provide some valuable information for field research to focus on measuring critical interactions, the relative strengths of which determine the potential for alternative states in community dynamics.

Note that in this study we only consider the qualitative aspect of long-term shifts in system equilibrium. Thus, our approach can only complement field experiments or specific quantitative models because it does not cover some essential aspects related to alternative states in ecological dynamics, in particular the nature of the transition trajectory from one state to the other or the characterisation of key thresholds in system dynamics (Scheffer et al., 2001). Nonetheless, a qualitative analysis of community feedback provides the means for managers to understand the underlying dynamics of an ecosystem, predict its potential for alternative states, and identify effective ways to intervene to minimise the likelihood of a shift to a particular state.

2.5.3 Model structure uncertainty

Models A to D demonstrate how structural uncertainty, i.e. the inclusion of uncertain interactions $a_{4,3}$ (RL—∘AB) and $a_{4,1}$ (CR—∘AB), can significantly affect model predictions and should not be underestimated in model building. However, in our examples with the Tasmanian rocky reef system, structural uncertainty does not affect the gross dynamics

of overstorey models, as the sign structure associated with the variables involved in the positive feedback driving the dynamics was unchanged in the adjoint matrices of all models A to D. Nonetheless, with the inclusion of these interactions in models B to D, the predicted responses of abalone to inputs in seaweed, lobster or sea urchin abundances become ambiguous as opposed to fully-determined in model A. A positive input in the abundance of lobster has a positive effect on abalone population in model A. The same input will induce the opposite effect in model B, however, if the negative effect $a_{4,3}$ of rock lobster on abalone is strong. For example, a decline in the density of emergent abalone was observed in the Maria Island marine reserve (Fig. 2.4b; Barrett et al., 2009) after recovery of a population of large lobsters. Large lobsters can directly prey on juvenile abalone and induce cryptic predator-avoidance behaviour among medium-sized individuals, and thus restrict their access to food (Pederson et al., 2008). The interaction $a_{4,1}$ (the local effect of the sea urchin on abalone in intact seaweed beds) was identified through small-scale experiments (Strain, 2009), but its effects on community dynamics (Model C) have not been reported at larger scales in the field. Thus in models B to D, depending on the relative strength of interactions $a_{4,1}$, $a_{4,2}$, $a_{4,3}$, the sign of abalone response to inputs can be switched and a similar perturbation can lead to opposite predictions about abalone abundances relative to model A.

In the ecological modelling literature, testing for uncertainty in ecological models often focuses on sensitivity analysis of parameter values (Saltelli et al., 2000) while the question of model structure uncertainty usually remains underestimated at best or unaddressed (Laskey, 1996; Dambacher and Ramos-Jiliberto, 2007; Hosack et al., 2008). We emphasise the importance of assessing structural uncertainty in models of complex systems, especially in ecological models where the understanding of system interactions is incomplete. Modellers often define confidence intervals around the mean values of model parameters to account for the robustness of the quantitative information supporting the model. Then, testing for model sensitivity to parameter values is recognised as essential (Saltelli et al., 2000). In the same manner, ranking the robustness of the qualitative information (e.g. ecological interactions) used in model building is essential to test every assumption built into the model structure itself. As illustrated here with models A to D, qualitative modelling of feedback properties is well suited to assess structural uncertainty in models of complex systems (Hosack et al., 2008; Metcalf et al., 2008). Perhaps most importantly, recognition of structural uncertainty in models and resolution of the effect of that

uncertainty on qualitative dynamics is extremely valuable to modellers and managers alike in prioritising future research.

2.6 Conclusions

In our qualitative models of subtidal reef communities in Tasmania, dominant positive feedback structures the relative responses of variables to long-term perturbations and qualitative predictions are consistent with observed alternative states. In the overstorey models, perturbations reinforce either a productive seaweed bed state favourable to commercial species, or a low-productive urchin barren state. In the understorey models, qualitative adjoint matrices agree with sustained changes in population growth rate promoting either a pink-benthos dominated state with high abundance of abalone and seaweed bed, or a brown-benthos dominated state. The conditions specified for each model inform the relative balance required between positive and negative feedback for system dynamics to display alternative states.

We illustrate with both a theoretical framework and empirical models of rocky reefs communities around Tasmania how qualitative modelling of feedback properties can identify mechanistic causal relationships between positive feedback and the presence of alternative states in ecosystem dynamics. Thus, based upon only qualitative knowledge of key variables and interactions, the approach can detect the potential for alternative states in ecosystem dynamics and inform the need for both caution in management of human activities that affect key variables, and also field experimentation to further investigate their existence. As illustrated with these Tasmanian examples, the approach can provide valuable insights on the indirect effects of human activities on ecosystem state and qualitative predictions can help distinguish the most adequate variables for both ecosystem monitoring and management intervention.

Chapter 3

Pattern-oriented validation and sensitivity analysis of a model with alternative community states: A simulation model of ecological dynamics of temperate rocky reefs in Tasmania

3.1 Abstract

While they can be very useful to support decision-making in ecosystem management, robust simulation models of ecosystems with alternative states are challenging to build and validate. Because of the possibility of alternative states in model dynamics, no trivial criteria can provide reliable and useful metrics to assess the goodness-of-fit of such models. This paper outlines development of the model TRITON, and presents some simulation-based validation and analysis of model sensitivity to input parameters. TRITON is a model of the local dynamics of seaweed-based rocky reefs communities in eastern Tasmania, which now occur in two alternative persistent states, either as dense and productive seaweed beds, or as sea urchin 'barren' habitat, i.e. bare rock largely denuded of macroalgae and benthic invertebrates due to destructive overgrazing by sea urchins. Pattern-oriented-modelling, i.e. comparing patterns in model dynamics from Monte-Carlo simulations with direct observations of Tasmanian reef communities over large scales, provides a valuable approach to calibrate the dynamics of TRITON.

Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test, we identify sea urchin and rock lobster recruitment rates, as well as lobster fishing as key parameters of influence on overall model behaviour. Through a set of independent sensitivity tests, we tease apart different sets of drivers facilitating the 'forward' shift from the seaweed bed to the urchin-dominated state, and the reverse shift from denuded sea urchin barren to recovery of barrens back to the seaweed cover. If solely

relying on rock lobsters to deplete sea urchins once barrens have established, chances of restoring seaweed beds are marginal: seaweed bed restoration takes up to three decades in the simulations and is unrealistic to implement under current fishery management plans. This model validation exercise provided both a better understanding of the key drivers of community dynamics (e.g. fishing of rock lobsters), and an assessment of priority areas for further empirical work identified from limitations of the model arising as a result of incomplete understanding of seaweed-urchin-lobster dynamics.

3.2 Introduction

Models of ecological dynamics can be helpful to inform decision-making and improve the management of human activities that rely on natural resources (Clark et al., 2001; Smith et al., 2011). More specifically, simulation models constitute unique decision-support tools to assess the effects of different management scenarios in ecosystems with alternative community states, where anthropogenic effects can lead to dramatic and possibly irreversible changes in structure and function across entire landscapes (Scheffer et al., 2001; Mumby et al., 2007; Firn et al., 2010; Melbourne-Thomas et al., 2010; Estes et al., 2011; Fung et al., 2011). However, building reliable simulation models requires a comprehensive understanding of key processes and drivers of system dynamics, and the accuracy of simulations will depend on the robustness of model parameterisation. Ecological processes, especially trophic interactions, are by essence variable and the dynamics of systems can be sensitive to this variation. However, ecological processes are usually difficult to measure precisely (Novak, 2010). It follows that even in well-studied ecosystems, a complete and precise understanding and quantification of ecological processes is rarely possible. Thus, uncertainty arises as a major feature of ecological models, stemming from the variable nature of ecological processes, from imperfect understanding of the mechanisms underpinning ecosystem dynamics, and limited ability to quantify complex natural processes with precision (Saltelli et al., 2000).

In this context, useful 'minimum realistic' ecological models must adequately address questions of interest to management while accounting for the amount and reliability of the information available about the study system (Fulton et al., 2003*a*). The art of ecosystem modelling lies in making a series of choices and, to a certain degree, an ecological model is only as reliable as the modeller's understanding of system dynamics (Klepper,

1997; Boschetti et al., 2011). Therefore, a simulation model requires some objective assessment prior to its application and several approaches are available to validate and calibrate the dynamics of complex ecosystem models (Klepper, 1997; Turley and Ford, 2009; Duboz et al., 2010). Model calibration is often undertaken by optimising the fit of simulated community dynamics to available empirical observations. Snapshots or mean observations about the composition of the study system are often used as metrics for model validation (e.g. mean species biomasses; Marzloff et al., 2009), although these model fitness criteria poorly characterise the variability of system dynamics, which may be of critical importance. In ecosystems that exhibit alternative states, ecologists exhaustively study and describe communities in one state or the other, while discontinuous shifts in community dynamics are, by definition, swift and are thus rarely observed or monitored (Scheffer et al., 2001). Therefore, precise information of a system with hysteresis (i.e. where a small change in parameters or species abundance can lead to a dramatic shift to a new community state that persists even when the change is reversed; see Donahue et al., 2011) at its threshold points is usually lacking. Lack of observations of community dynamics for systems that manifest hysteresis, make validation of ecosystem models with alternative states particularly challenging (Scheffer and Carpenter, 2003 but see Mumby et al., 2007; Lauzon-Guay et al., 2009; Fung et al., 2011 for examples of model validation).

Given inability to formally and comprehensively validate the accuracy of ecosystem models against reality, predictions from ecosystem models are inherently uncertain. Uncertainty of simulation models can be broken down into three main components:

(i) structural uncertainty, which refers to model structure and its resolution, e.g. the extent to which species are aggregated or the nature of functional groups; the number and certainty of trophic interactions considered; spatial and temporal scales of processes, etc. (Laskey, 1996; Hosack et al., 2008; Marzloff et al., 2011*a*);

(ii) choice of model formulation, which includes programming choices (e.g. discrete versus continuous time (Deng, 2008), timing of processes operating at different scales; whether the model is spatially explicit) as well as the actual representation of ecological processes in the model (e.g. alternative ways to account for density-dependence in functional responses; Skalski and Gilliam, 2001);

(iii) uncertainty in model parameterisation; uncertainty in individual parameter

estimates, which can rapidly compound depending on interactions in the model, directly contributes to uncertainty of model outputs (Saltelli et al., 2000; Cariboni et al., 2007).

Assessing these different sources of model uncertainty is an essential ingredient of ecological modelling (Saltelli et al., 2000; Marzloff et al., 2011*a*). An added complication for models with alternative community states is that sensitivity analysis can be of limited value (van Nes and Scheffer, 2003). This is because simulation outcomes may only reflect whether the community reaches one state or the other and only partially depict hysteresis in model dynamics. Additionally, the modelled community is more prone to shift to the alternative state when parameter space is near bifurcation points, so linear and partial sensitivity tests can be limited because they typically neglect the influence of interactions between multiple input parameters giving rise to complex non-linear dynamics (Saltelli et al., 1999; van Nes and Scheffer, 2003).

In this paper, we explore and validate the behaviour of a model of subtidal seaweed-based reef community dynamics in eastern Tasmania, south east Australia. These temperate rocky reefs occur in two alternative community states, as dense stands of seaweed or as bare rocky expanses known as sea urchin 'barren' habitat (Ling et al., 2009*a*). On the east coast of Tasmania, the climate-driven range extension of the long-spined sea urchin *Centrostephanus rodgersii* represents a major threat for endemic seaweed bed communities, including high value commercial species (Johnson et al., 2005; Ling et al., 2009*a*). Within its' new eastern Tasmanian range, *C. rodgersii* can form and maintain extensive barren habitat, i.e. areas of bare rock up to 10s ha, following the destruction of seaweed beds by its grazing activity. Compared to the seaweed beds, sea urchin barrens have dramatically lower productivity, habitat complexity and species diversity (Ling, 2008), and key fishery species (abalone and rock lobsters) do not occur in commercially harvestable quantities. Thus, preventing the formation of further *C. rodgersii* barrens, and promoting the reverse shift back to seaweed communities where barrens occur, is a priority for the management of reef communities and fisheries in eastern Tasmania (Ling et al., 2009*a*; Pecl et al., 2009). It is therefore important that managers are aware of the existence of fundamentally different ecologies in each alternative states and that they better understand the ecological mechanisms that drive the shift from dense seaweed bed to urchin barrens, and the

circumstances in which these shifts are likely to occur. Here, we calibrate and validate model behaviour against observed patterns that describe community dynamics, including shifts between these alternative states. Structural uncertainty has been comprehensively tested in this model (Marzloff et al., 2011*a*) and hence this paper focuses on sensitivity to uncertainty in model formulation and parameterisation. Using Monte-Carlo simulations, we explore the effects of parameter uncertainty on the behaviour of the model. The objectives of this work are three-fold.

(i) First, to calibrate the propensity of the simulated community to shift from the seaweed bed to the sea urchin barren state against known probability of barren formation in southeastern Australia. In addition, comparison of the dynamics emerging from Monte-Carlo simulations against observed patterns contributes to model validation.

(ii) To quantify model sensitivity using the extended Fourier amplitude sensitivity test (FAST), a quantitative model-independent sensitivity analysis technique for complex simulation models (Saltelli et al., 1999). The extended FAST assesses the contribution to model output of each input parameter, including through interactions with other factors. We analyse model global behaviour as well as specific components of its dynamics: by decomposing overall model dynamics into 'forward' shift (from seaweed bed to barren) and 'backward' shift (from barren back to seaweed bed) components, the sensitivity tests overcome problems inherent to sensitivity analysis of models with hysteresis (van Nes and Scheffer, 2003).

(iii) To use model sensitivity analysis as a means to both, identify key ecological processes that drive Tasmanian reef community dynamics, and highlight gaps in knowledge about processes of high influence on community dynamics. In this respect, model sensitivity analysis provides a valuable tool to guide and prioritise future experimental and other empirical ecological research on Tasmanian rocky reefs.

3.3 Material and Methods

We developed a simulation model of Tasmanian reef communities, which we have called TRITON (Temperate Reefs In Tasmania with lObsters and urchiNs), to test the ecological

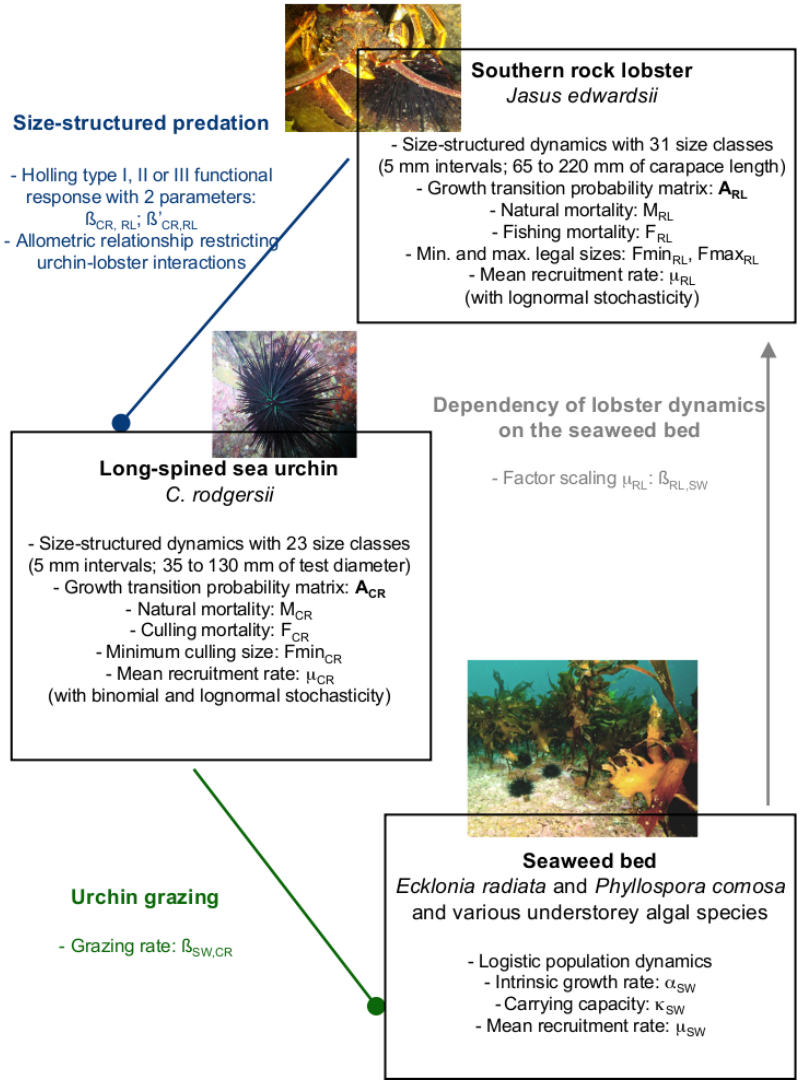


Figure 3.1: Conceptual diagram of TRITON, a model of local community dynamics on rocky reefs in eastern Tasmania. The boxes represent the three functional groups or species explicitly interacting in TRITON, namely southern rock lobster, long-spined sea urchin and the seaweed assemblage. Each box lists all the parameters defining the dynamics of each group. Interactions between the three groups are represented as arrows, where a full circle at the end of lines indicates a negative effect to the adjacent group while an actual arrow head points to a group positively affected in this interaction. Photography credits: Scott D. Ling.

consequences of different management scenarios. Currently, a major concern for the management of Tasmanian subtidal reef communities is the formation of sea urchin barrens following incursion of the long-spined sea urchin *Centrostephanus rodgersii* from Australia's mainland to Tasmanian waters (Ling et al., 2009*a*). By destructively grazing seaweeds and benthic invertebrates, *C. rodgersii* can form extensive barren areas denuded

of macroalgal cover, with flow-on effects reducing local abundances of the two most valuable commercial reef species in Tasmania (southern rock lobster, *Jasus edwardsii* and blacklip abalone, *Haliotis rubra*) (Johnson et al., 2005). Large lobster individuals (carapace length >140 mm) constitute the only efficient predators of *C. rodgersii* in Tasmanian waters (Ling et al., 2009*a*), so that commercial and recreational fishing of lobster directly facilitates the formation of *C. rodgersii* barrens. If simulation modelling is to support the management of this ecological phenomenon, the ability of TRITON to realistically capture the potential for discontinuous shifts between the two alternative states (seaweed bed versus sea urchin barren) is essential. The following subsections describe the structure of the TRITON model, its parameterisation and the empirical data available to calibrate model dynamics. Next, we outline the extended Fourier amplitude analysis test (FAST; Saltelli et al., 1999) used to test model sensitivity to parameter values, before specifying both the simulation characteristics and the important output metrics screened for the sensitivity tests.

3.3.1 TRITON: local dynamics of Tasmanian rocky reef communities

TRITON represents the mean community dynamics of an individual patch of rocky reef (area 100 m^2 - 10 ha; depth 8 - 35 m on open exposed reef habitat where *C. rodgersii* barrens occur in Tasmania). The dynamics of three functional groups or species are explicitly captured (Fig. 3.1): each difference equation respectively represents the dynamics of the seaweed bed (as SW in the equations) (Eq. 3.1), sea urchin (as CR for *Centrostephanus rodgersii*) (Eq. 3.2) and rock lobster (as RL) (Eq. 3.3). Size-structured dynamics for both sea urchin and rock lobster populations are key for TRITON to realistically capture both, the effects of size-related fishing regulations (i.e., legal catch size), and the size-structured nature of lobster predation on urchin (cf. Eq. 3.2).

(i) The seaweed bed includes all canopy-forming macroalgae (dominated by *Ecklonia radiata* at depth> 6 m, or *Phyllospora comosa* on shallow reef, and including a raft of other large phaeophytes that contribute to the canopy structure including representatives of the genera *Cystophora*, *Sargassum*, *Sierococcus*, *Carpoglossum*, *Acrocarpia* and *Xiphophora*) and understorey algal assemblages (e.g. filamentous and foliose rhodophyta, small foliose chlorophyta and phaeophyta, and corallines

and other encrusting red algae). Quantitative information on the dynamics of the different guilds of algae that constitute the seaweed bed is lacking. The understanding of the details of overgrazing of these different algal species and groups by *C. rodgersii* is also incomplete. Thus, in the model, the seaweed bed compartment corresponds to the current minimum realistic representation of temperate algal communities. Seaweed assemblage (SW in the following equations) dynamics follows logistic growth (Eq. 3.1), with parameters derived from monitoring of macroalgal recovery from a barren state over two years following the experimental removal of grazers (Ling, 2008). Propagules supply is constant and assumed independent from the local state of the seaweed bed, as external supply from adjacent macroalgal beds is not limiting (CR Johnson, personal observation). Although a range of herbivorous species rely on macroalgae as part of their diet, only the long-spined sea urchin *Centrostephanus rodgersii* (CR) has demonstrated the ability to overgraze Tasmanian seaweed beds on exposed rocky reefs on the open coast. The native purple sea urchin (*Heliocidaris erythrogramma*) also forms barren habitat (on a smaller scale than *C. rodgersii*) in sheltered bays in eastern Tasmania, but TRITON focuses exclusively on the dynamics of inshore exposed reefs where the effect of *H. erythrogramma* is marginal. Thus, grazing by the long-spined sea urchin is the only explicit source of seaweed biomass loss in the model. Urchin grazing rate is assumed to be constant as, contrary to northern hemisphere strongylocentroid urchins that destructively graze seaweed by forming a grazing front once critical density and behavioural thresholds are reached (Lauzon-Guay et al., 2009), there is no evidence of density-dependence on *Centrostephanus rodgersii* grazing rate. Indeed, the effects of individual grazers are additive: on barren habitat, sea urchin destructive grazing shows a remarkably consistent ratio of 0.6 m^2 of grazed area per individual, irrespective of the size of the barrens patch (Flukes et al., unpublished data). Although all size classes of emergent urchins consume seaweed at exactly the same rate for a given biomass of urchins (the last term in Eq. 3.1), larger urchin individuals have a high destructive impacts on standing macroalgae in the model as urchin population dynamics (see Eq. 3.2) capture biomass gain from one size class to the next due to individual growth.

The equation for the seaweed assemblage is given as:

$$SW_{t+1} = max(0, r_{SW} + SW_t \times (1 + \underbrace{\alpha_{SW} \times \frac{K_{SW} - SW_t}{K_{SW}}}_{\text{Logistic growth}}) - \underbrace{\beta_{SW,CR} \times \sum_{s=1}^{N_{CR}} CR_{s,t}}_{\text{Loss to sea urchin grazing}}) \quad (3.1)$$

with SW_t, seaweed biomass at time t (g. 200 m^{-2}); r_{SW}, seaweed recruitment rate (g. $year^{-1}$. 200 m^{-2}); α_{SW}, seaweed intrinsic growth rate ($year^{-1}$); K_{SW}, seaweed carrying capacity (g. 200 m^{-2}); $\beta_{SW,CR}$, sea urchin grazing rate (g of SW. g of CR^{-1}. $year^{-1}$. 200 m^{-2}); $CR_{s,t}$, biomass density of sea urchin (CR for *C. rodgersii*) in size class s at time t (g. 200 m^{-2}).

(ii) Population growth of *C. rodgersii*, the long-spined sea urchin, is size-structured (Eq. 3.2) and fitted against data from large-scale population surveys on the east coast of Tasmania (cf. Appendix A; Ling et al., 2009*b*; Johnson et al., 2011). Despite its destructive grazing of seaweed beds, sea urchin population dynamics (CR for *Centrostephanus rodgersii* in the equations) is independent of seaweed consumption because sea urchins forage on drift material, ephemeral filamentous algae and microalgae to subsist on barren habitat in the absence of attached macroalgae (Ling and Johnson, 2009). In TRITON, the size structure of sea urchin individuals is distributed across 21 size classes ranging from 40 to 120 mm test diameter using 4.12 mm increments, while individuals smaller than 40 mm are not considered because they stay cryptic in crevices with virtually no effect on standing macroalgae through grazing (SD Ling, unpublished data; Ling and Johnson, In press; Ling et al., 2009*a*). The effect of habitat complexity on survival of juveniles (provision of crevices to shelter from predation) is implicitly modelled in the Monte-Carlo simulations through changes in mean recruitment rate. Only adult animals of test diameter superior to 70 mm are fully emergent (Ling and Johnson, In press; Ling et al., 2009*a*), hence it is these animals that are exposed to lobster predation in the model. Recruitment is stochastic and external given that *C. rodgersii* has a planktotrophic larval stage of c. 3 months duration that can therefore disperse with currents at scales of 100-1000 km (Huggett et al., 2005; Banks et al., 2007). The southern rock lobster is the only effective predator of the spiny sea urchin in Tasmanian waters. Because a lobster's ability to handle a given size of sea urchin is determined by the size of its front pair of walking legs (Ling et al., 2009*a*), predation of *C. rodgersii* by rock

lobster is constrained by the relative size of prey and predator (Eq. 3.2). Hence, size-structured predation by lobsters (third term of Eq. 3.2) is the only explicit source of natural mortality on sea urchins in the model. The predation rate $\beta_{CR,RL}$ accounts for density-dependence of *C. rodgersii* predation following any of Holling's type I, II or III functional response (Holling, 1966; cf. Appendix A for further details about the definition and parameterisation of Holling's functional responses in TRITON).

$$
\begin{aligned}
CR_{s,t+1} = max \Bigg(0, & \underbrace{r_{CR}}_{\text{Recruitment to the first size class (Only if s = 1)}} \\
& + \underbrace{CR_{s,t} \times exp(-\beta_{CR})}_{\text{Biomass at t affected by natural mortality}} \\
& + \underbrace{\sum_{j=1}^{j<s} \delta'_{s,j} \times CR_{j,i} - (\sum_{i>s}^{N_{CR}} \delta_{i,s}) \times CR_{s,t}}_{\text{Growth between different size classes accounts for individual weight gain}} \\
& \underbrace{- \beta_{CR,RL} \sum_{i=min_{CL}}^{N_{RL}} RL_{i,t}}_{\text{Size-structured predation}} - \underbrace{CR_{s,t} \times (1 - exp(-F_{CRs}))}_{\text{Culling mortality}} \Bigg)
\end{aligned}
\tag{3.2}
$$

with $CR_{s,t}$, biomass of sea urchin in size class s at time t (g. 200 m^{-2}); r_{CR}, urchin recruitment rate to the first size class $s = 1$ (g. year^{-1}. 200 m^{-2}) where the mean recruitment rate μ_{CR} varies stochastically: the probability of any recruitment a given year follows a binomial of probability p_{CR} of successful recruitment; when recruitment occurs a given year, its magnitude is drawn out of a lognormal distribution of mean 0 and standard deviation σ_{CR}; β_{CR}, urchin natural mortality (year^{-1}); F_{CR}, urchin harvesting mortality (year^{-1}); $\delta_{i,j}$, biomass-based growth transition probability from size class j to i (year^{-1}); $\delta'_{i,j}$, abundance-based growth transition probability from size class j to i (year^{-1}); $\beta_{CR,RL}$, size-structured lobster predation rate on sea urchin of size class s (g of CR. g of RL^{-1}. year^{-1}. 200 m^{-2}), which follows any of Holling's type I, II or III functional responses. Only lobsters from size classes bigger than min_{CL}, defined from the following allometric relationship, can prey on sea urchins of class s: the minimum carapace length (CL_{min}, in mm) for rock lobster to predate upon sea urchin individuals of a given test diameter (TD, in mm) can be expressed after Ling et al. (2009*a*) as: $CL_{min} = \alpha_1 log(TD) - \alpha_2$ where the scalars α_1 and α_2

define the allometry of the size-structured interaction.

(iii) The size-structured lobster (RL for rock lobster) population component is derived from the Tasmanian rock lobster fishery stock assessment model (see Punt and Kennedy, 1997; McGarvey and Feenstra, 2001), and so TRITON represents the lobster population across 31 size classes ranging from 65 to 215 mm of carapace length by 5 mm increments. This also enables a realistic representation of the effects of size-related fishing regulations (since minimum or maximum legal catch sizes are to the nearest 5 mm). This representation of size-structured dynamics enabled close fitting against observed population recovery from fishing following protection from fishing (Barrett et al., 2007). The natural mortality term accounts for sources of mortality that are not explicitly captured elsewhere in the equation, e.g. through predation by sharks or cephalopods (Pecl et al., 2009). The lobster population in the model relies on the local state of the seaweed bed as an essential source of habitat and food. More specifically, abundances of juveniles are lower on barren habitat than in adjacent kelp beds, while initial observations suggest that abundances of large predatory-capable lobsters seems largely unaffected by barren habitat (Johnson, unpublished data). Indeed, canopy-forming macroalgae, as opposed to barren habitat, can facilitate both, settlement of lobster puerulus by providing a complex three-dimensional structure and (by inference) an appropriate settlement cue, and development of juvenile lobsters by supporting a broad diversity of invertebrate species (Ling, 2008). Therefore, a constant coefficient, ranging from 0 (for no recruitment on barren habitat) to 1 (for no effect of barrens on recruitment), scales lobster recruitment as a function of the state of the seaweed bed (cf. last term of Eq. 3.3). Lobster recruitment rate r_{RL} is (i) stochastic following a lognormal stochastic function and (ii) independent of the local lobster population given that lobsters have an 18-24 month pelagic larval stage, implying large-scale dispersal

(Bruce et al., 2007). The equation is:

$$RL_{s,t+1} = max\left(0,\ \underbrace{r_{CR}\left[1-(1-\beta_{RL,SW}(1-\frac{SW_t}{K_{SW}}))\right]}_{\text{Recruitment to the first size class (Only if s = 1) gets reduced as barren habitat expands.}}\right.$$
$$+\ \underbrace{\sum_{j=1}^{j<s}\delta'_{s,j}\times RL_{j,i}-(\sum_{i>s}^{N_{RL}}\delta_{i,s})\times RL_{s,t}}_{\text{Growth between different size classes accounts for individual weight gain}}$$
$$\left.+\ \underbrace{RL_{s,t}\times exp(-\beta_{RL})}_{\text{Biomass at t affected by natural mortality}}\ \underbrace{-\,RL_{s,t}\times(1-exp(-F_{RLs}))}_{\text{Fishing mortality}}\right) \tag{3.3}$$

where $RL_{s,t}$ denotes the biomass of rock lobsters in size class s at time t (g. 200 m^{-2}); r_{RL}, lobster recruitment rate (g. $year^{-1}$. 200 m^{-2}) in which mean recruitment rate μ_{RL} varies stochastically following a lognormal stochastic function of mean 0 and standard deviation σ_{RL}; $\beta_{RL,SW}$ is a scalar, ranging from 0 for no lobster recruitment on barren grounds to 1 for no effect of barren habitat on lobster mean recruitment; β_{RL}, lobster natural mortality ($year^{-1}$); $\delta'_{s,j}$, biomass-based transition probability from size class j to s, or element of the s^{th} row, j^{th} column of the transition probability matrix ($year^{-1}$ or g. g^{-1}. $year^{-1}$); $\delta_{i,s}$, abundance-based transition probability from size class s to i ($year^{-1}$ or individual.$individual^{-1}$.$year^{-1}$); SW_t, seaweed biomass (g. 200 m^{-2}); F_{RLs}, fishing mortality for lobster of class s ($year^{-1}$).

Recruitment rates vary stochastically for both lobster and sea urchin populations (See Eq. 3.2 and 3.3), while propagule supply is assumed constant for the seaweed bed (Eq. 3.1). Recruitment is independent of local spawning population densities. For all three modelled groups, larval / propagule settlement occurs over much larger spatial scales than individual reefs, and hence is not limited locally (Banks et al., 2010; Linnane et al., 2010; Coleman et al., 2011; Johnson, unpublished data). Both the sea urchin and lobster have lengthy larval phases (∼3 and 18-24 months respectively) during which time they can be transported far from their natal reef, and sporogenous seaweeds are often torn from the substratum in storms and drift along the coast depositing spores. The three-dimensional seaweed bed provides both essential substratum for lobster puerulus settlement and a diversity of food sources for juvenile lobsters (Ling, 2008), and so lobster recruitment is affected by the extent of barren habitat (Eq. 3.3).

Model time is discrete because it is more computationally efficient than using continuous time, and also more flexible to implement using the object-oriented Python programming language (Python Software Foundation, 2008). A two-week time-step was adopted as a compromise between computational efficiency and adequate convergence between discrete- and continuous-time dynamics (Deng, 2008).

3.3.2 Parameterisation

Variables are expressed in fresh weight biomass density with a default parameterisation for a reef area of 200 m^2 (variables in g. 200 m^{-2}). Biomass density allows for weight-based (rather than abundance-based) trophic interactions and was derived from experimental or other empirical observation (see Appendix A). All modelled processes were parameterised from in situ observations or measurements (Redd et al., 2008; Ling and Johnson, 2009), field- or laboratory-based experiments (Hill et al., 2003; Ling et al., 2009*a*), or well-validated models (Punt and Kennedy, 1997). For each parameter, Table 3.1 summarises data sources (Punt and Kennedy, 1997; Punt et al., 1997; McGarvey and Feenstra, 2001; Hill et al., 2003; Ling, 2008; Barrett et al., 2009; Ling and Johnson, 2009; Ling et al., 2009*a*,*b*) and the estimated distribution of each parameter value (i.e. mean and standard deviation for normal distributions; minimum and maximum bounds for uniform distributions). For normally distributed parameters, values within the 90% confidence interval (bounded by the 5 and 95% quantiles) were explored during the sensitivity analyses. As well as enveloping uncertainty in modelled processes, these ranges implicitly encompass the span of environmental conditions (e.g. habitat, depth) and anthropogenic forcing (e.g. fishing pressure) encountered on Tasmanian rocky reefs. Appendix A comprehensively describes all data sources and the estimation of model parameters.

Table 3.1: Parameter estimates (mean and standard deviation for normally-distributed errors; mean, minimum and maximum estimates otherwise) and ranges (90% confidence intervals for normally distributed estimates) used for the sensitivity analysis of the TRITON model of Tasmanian reef dynamics. The table lists all parameters defining population dynamics of the three model groups (i.e. seaweed bed, urchin, lobster), trophic interactions and allometric relationships in the model.

Parameter	Units	Estimate	Standard error	Confidence interval
Seaweed bed logistic growth				
Fitted against data from Ling, 2008.				
α_{SW}	year^{-1}	4.43	1.65	$1.72 - 7.14$
K_{SW}	g SW.200 m^{-2}	3.4×10^5	3.6×10^4	$2.8 \times 10^5 - 4 \times 10^5$
μ_{SW}	g SW.200 m^{-2}.year^{-1}	**5000**		$2500 - 10000$
with α, intrinsic growth rate; K, carrying capacity; μ, mean annual recruitment rate.				
Sea urchin size-structured population growth				
Growth transition matrix derived from Ling and Johnson, 2009.				
β is the annual natural mortality; μ, the mean annual recruitment rate.				
Fitted against data from Ling et al., 2009*b*; Johnson et al., 2011.				
β_{CR}	$year^{-1}$	**0.11**		$0.1 - 0.15$
μ_{CR}	g CR.200 m^{-2}.year^{-1}	**4100**		$2500 - 10000$
The annual stochastic recruitment function follows a binomial with a 0.4 probability of success, which is combined with a lognormal with a standard deviation σ_{CR} of 0.5.				
Lobster size-structured population growth				
Growth transition matrix derived from McGarvey and Feenstra, 2001.				
β is the annual natural mortality; μ, the mean annual recruitment rate.				
Fitted against data from Barrett et al., 2007.				
β_{RL}	$year^{-1}$	**0.23**		$0.20 - 0.26$
μ_{RL}	g RL.200 m^{-2}.year^{-1}	**350**		$200 - 800$
The annual stochastic recruitment function follows a lognormal with a standard deviation σ_{RL} of 0.6.				
Lobster dependency on the state of the seaweed bed				
Lobster recruitment is scaled by: $(1-\beta) \times (1 - \frac{B_{SW}}{K_{SW}})$				
with B_{SW}, seaweed bed biomass density; K_{SW}, seaweed bed carrying capacity.				
$\beta_{SW,CR}$	constant	0.64	0.11	$0.46 - 0.83$

Parameter	Units	Estimate	Standard error	Confidence interval
Urchin grazing rate				
$\beta_{SW,CR}$	g SW.g CR^{-1}.year^{-1}	5.94	1.10	4.13 – 7.75
Functional responses of lobster predation on urchin				
With B_{CR}, urchin biomass density (g. 200m^{-2}): Holling Type I as $\beta_{CR,RL} = min(\beta B_{CR}, \beta')$				
β	g RL^{-1}.year^{-1}	6.68 $\times 10^{-4}$	2.27 $\times 10^{-5}$	6.31 $\times 10^{-4}$ - 7.05 $\times 10^{-4}$
β'	g CR.g RL^{-1}.year^{-1}	9.40	3.00	4.46 - 14.33
Holling Type II as $\beta_{CR,RL} = \frac{\beta(B_{CR})}{1+\beta'(B_{CR})}$				
β	g RL^{-1}.year^{-1}	11.09$\times 10^{-4}$	1.68 $\times 10^{-4}$	8.34 $\times 10^{-4}$ - 13.85 $\times 10^{-4}$
β'	g CR^{-1}	1.10$\times 10^{-4}$	0.20 $\times 10^{-4}$	7.76 $\times 10^{-5}$ - 14.19 $\times 10^{-5}$
Holling Type III as $\beta_{CR,RL} = \frac{\beta(B_{CR})^2}{1+\beta'(B_{CR})^2}$				
β	g CR^{-1}.g RL^{-1}.year^{-1}	2.35 $\times 10^{-7}$	0.55 $\times 10^{-7}$	1.46 $\times 10^{-7}$ - 3.25 $\times 10^{-7}$
β'	g CR^{-1}.g CR^{-1}	2.50 $\times 10^{-8}$	0.60 $\times 10^{-8}$	1.47 $\times 10^{-8}$ - 3.60 $\times 10^{-8}$

Allometric and other size-based relationships

Length-weight relationship for the long-spined sea urchin
$B = 0.00267 \times TD^{2.534}$,
with B, urchin individual weight (g); TD, urchin test diameter (mm).

Length-weight relationship for the southern rock lobster
$B = 0.000271 \times CL^{3.135}$,
with B, lobster individual weight (g); CL, lobster carapace length (mm).

Size-Structured predation of lobster on urchin
$CL_{min} = 43.5 \times \log(TD) - \beta$, with $\beta \in [48.91 : 71.01]$
with CL, lobster carapace length (mm); TD, urchin test diameter (mm).

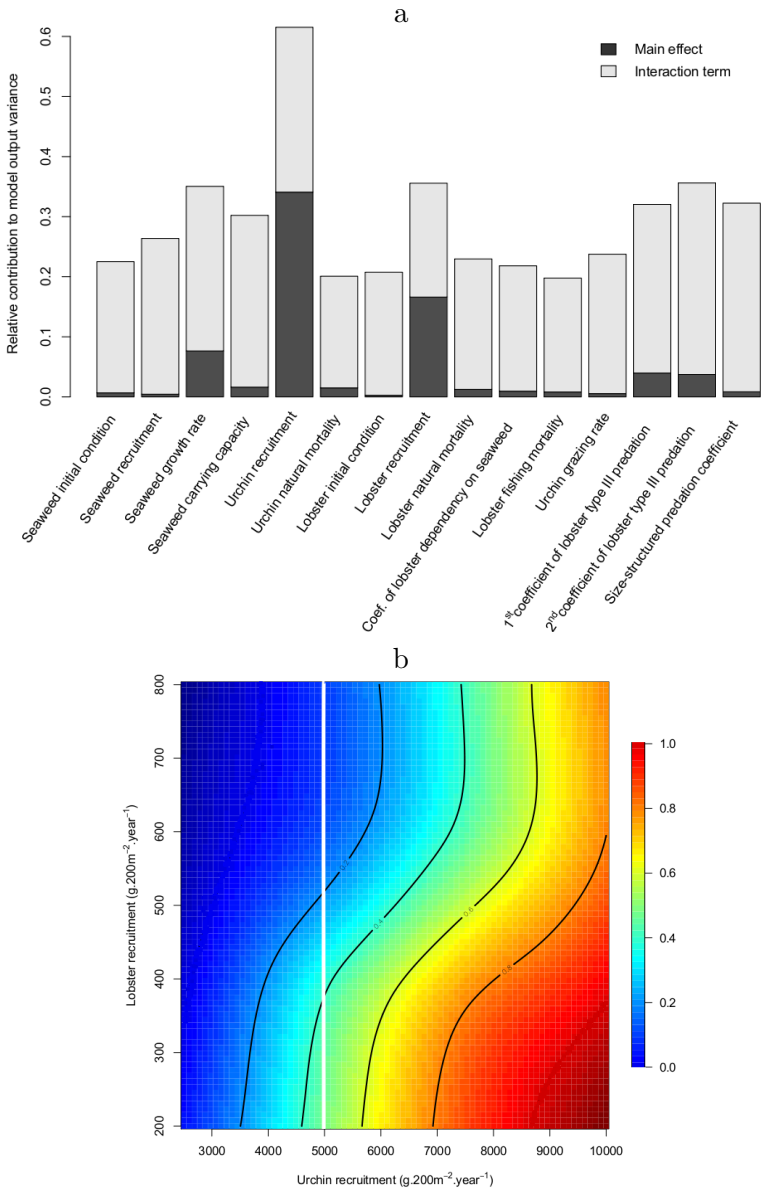


Figure 3.2: Sensitivity results from 50-year-long Monte-Carlo simulations for model calibration under historical fishing conditions. (a) Extended FAST sensitivity indices reveal that recruitment rates for urchin and lobster have the highest influence on model behaviour; (b) Surface plot of the probability of shift from seaweed bed to sea urchin barren as a function of urchin and lobster recruitment. The white vertical line marks the minimum mean recruitment rate that can produce realistic biomass densities of sea urchin and achieve levels of barren formation across simulations similar to those observed across rocky reefs in New South Wales (Andrew and O'Neill, 2000) and Tasmania (Johnson et al., 2005, 2011) where *C. rodgersii* is long established (i.e. 50% of rocky reef coverage).

3.3.3 Model validation

No meaningful optimisation could be designed to calibrate the goodness-of-fit of the model against multiple quantitative criteria (e.g. Klepper, 1997; Duboz et al., 2010). In particular, because of the occurrence of alternative states, aiming for model mean dynamics to capture mean community composition is not meaningful. Because of the model complexity, neither could an interpretable analytical solution be derived so as to formally validate the occurrence of alternative stable states within the estimated parameter space as was achieved, for example by Fung et al. (2011). Initially proposed as a means to calibrate agent-based models (Grimm et al., 2005), pattern-oriented modelling constitutes an effective way to validate and calibrate the behaviour of TRITON against the data available for Tasmanian reef dynamics. We focused on the ability of simulations to mimic observations on the two alternative community states and the dynamics of the 'forward' shift from the seaweed bed to the sea urchin barren state. The ranges of biomass densities of the three model groups were estimated for both community states from large surveys of reef habitat and species abundance around Tasmania. We converted seaweed percentage cover and sea urchin density to biomass densities directly comparable to model outputs (Fig. 3.5a). The frequency of occurrence of the two alternative states in different regions of the coastline with different fishing and urchin invasion history was derived from these surveys (Johnson et al., 2005, 2011). Historical fishing mortalities were estimated from the rock lobster stock assessment model (F_{RL} within 1-1.8 year^{-1}; Klaas Hartmann, pers. comm.). In regions where *C. rodgersii* has been present for several decades and where key reef predators have been depleted by fishing (e.g. New South Wales, the Furneaux group and north-eastern Tasmania), about 50% of coastal rocky reef habitat is reported as sea urchin barren (Andrew and O'Neill, 2000; Johnson et al., 2011). Recruitment, i.e. juveniles entering the population, is possibly the most challenging process to understand and measure in marine ecology and fisheries sciences. Thus, in marine ecosystem models, recruitment rates are widely recognised as the most uncertain parameters and are commonly used as calibration factors (e.g. Marzloff et al., 2009). Lobster predation directly controls sea urchin dynamics in TRITON so we adjusted *C. rodgersii* recruitment to ensure that simulations could achieve realistic sea urchin biomass densities while accurately producing 'forward' shifts from the seaweed bed to the urchin barren state. A pilot global sensitivity analysis was used to adjust sea urchin mean

recruitment rate (μ_{CR}; Eq. 3.2) to calibrate model behaviour under historical fishing patterns (Fig. 3.2). A final aspect of model validation specifically tested for alternative formulations of the lobster predation rate. Density-dependence of lobster predation rate on urchin density was successively represented as a Holling type I, II or III functional response (Holling, 1966), and the effects on model behaviour compared (Fig. 3.3). The effects of alternative formulations of lobster predation rate were also examined by comparing the scores on the first two axes of the PCA of simulation outcomes with each of the Holling type I, II or III functional responses. The comparison of the projection of simulations outcomes with each functional response on the first two PCs was both, qualitative based on the visual inspection (Fig. 3.4), and statistical using a MANOVA with the type of functional response as a factor.

3.3.4 Global sensitivity analysis with the extended Fourier amplitude sensitivity test (FAST) (Saltelli et al., 1999)

The extended Fourier amplitude sensitivity test (extended FAST) provides a robust quantitative and model-independent sensitivity analysis method for models of complex systems dynamics (Saltelli et al., 1999). Unlike correlation- or regression-based analysis techniques, the ANOVA-like extended FAST is suited to quantitative sensitivity analysis of complex non-linear models because it does not assume linearity or monotony between model inputs and outputs. With the extended FAST, parameter space is explored comprehensively following a Latin-Hypercube-Sampling-like stratified design (see Saltelli et al., 1999). In the absence of sufficient empirical data to derive distributions, and to sample extremes as frequently as mean values, we assumed uniform distributions for input parameters within the bounds given in Table 3.1. The extended FAST assigns a unique frequency to each input parameter. These frequencies define the cyclic exploration of each parameter's range through successive Monte-Carlo simulations. Thus the extended FAST computes the relative contribution of each input to the variance of the output using multidimensional frequency decomposition that, again, is free of assumptions about model behaviour. The contribution of each input is reported as a total sensitivity index. This index includes both the main effect attributable to that parameter and higher degree effects from interactions with other parameters. Higher degree interactions often contribute more than the primary effect of any individual parameter to variance in model output, so these total sensitivity indices are useful to quantify a parameter's overall influence on

the dynamics of complex ecosystem models (Saltelli et al., 1999). The extended FAST method was implemented using the *sensitivity* package of the R software for statistical computing (R Development Core Team, 2010). Using *Rpy2*, a high-level interface between R and Python (Python Software Foundation, 2008), we automated all sensitivity analyses between R and the TRITON simulation model. Each parameter range was divided into 500 levels. This resolution was adopted following preliminary tests of the sensitivity of the extended FAST. This brought the total number of Monte-Carlo simulations per test to $500 \times n$, where n refers to the number of input parameters screened.

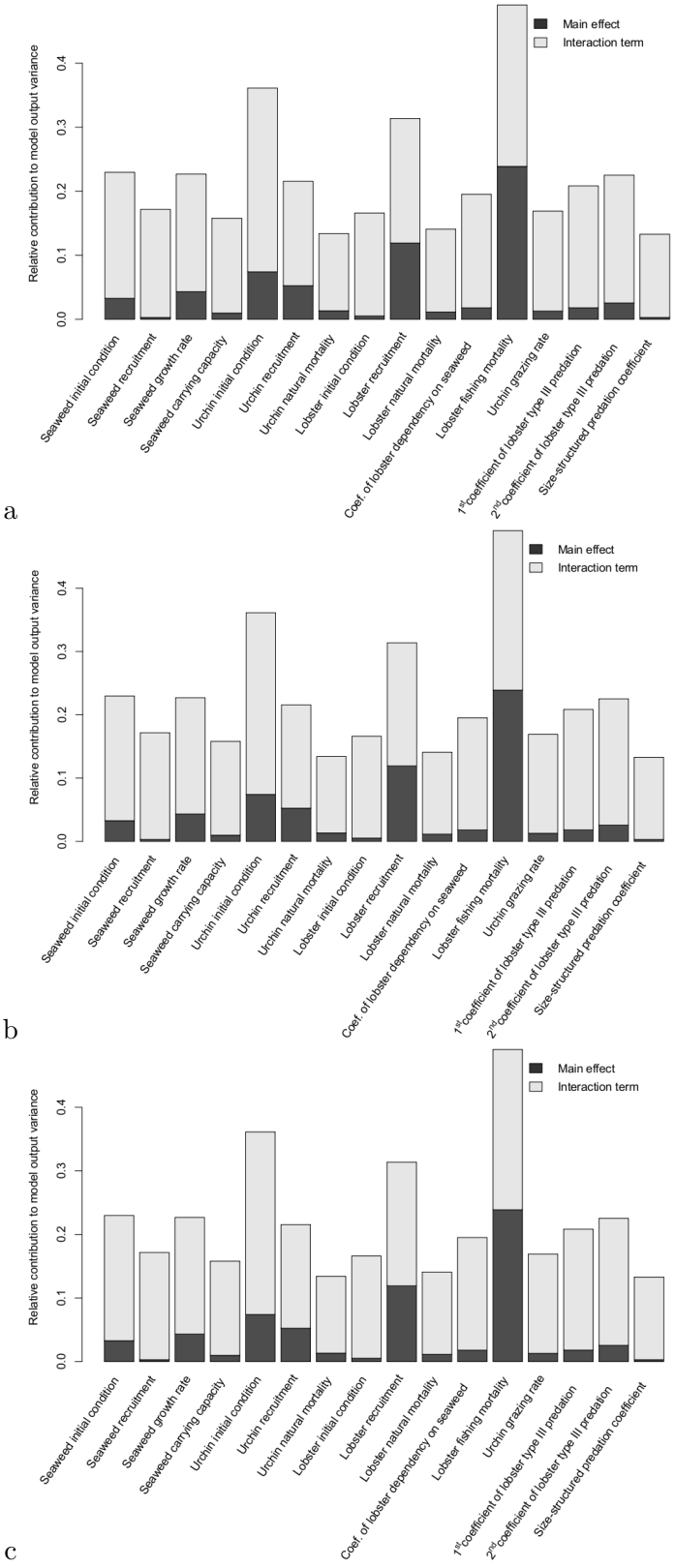


Figure 3.3: Extended FAST indices quantifying the contribution of input parameter values to model output variance, using the first principal component from the PCA (accounting for 77% of the total variance) on mean-centred normalised biomass density outputs, under alternative formulations of the functional response of lobster predation on sea urchin, assuming either Holling type I (a), II (b) or III (c) relationships. Fig. 3.4 provides a graphical summary of final model state across the three model groups.

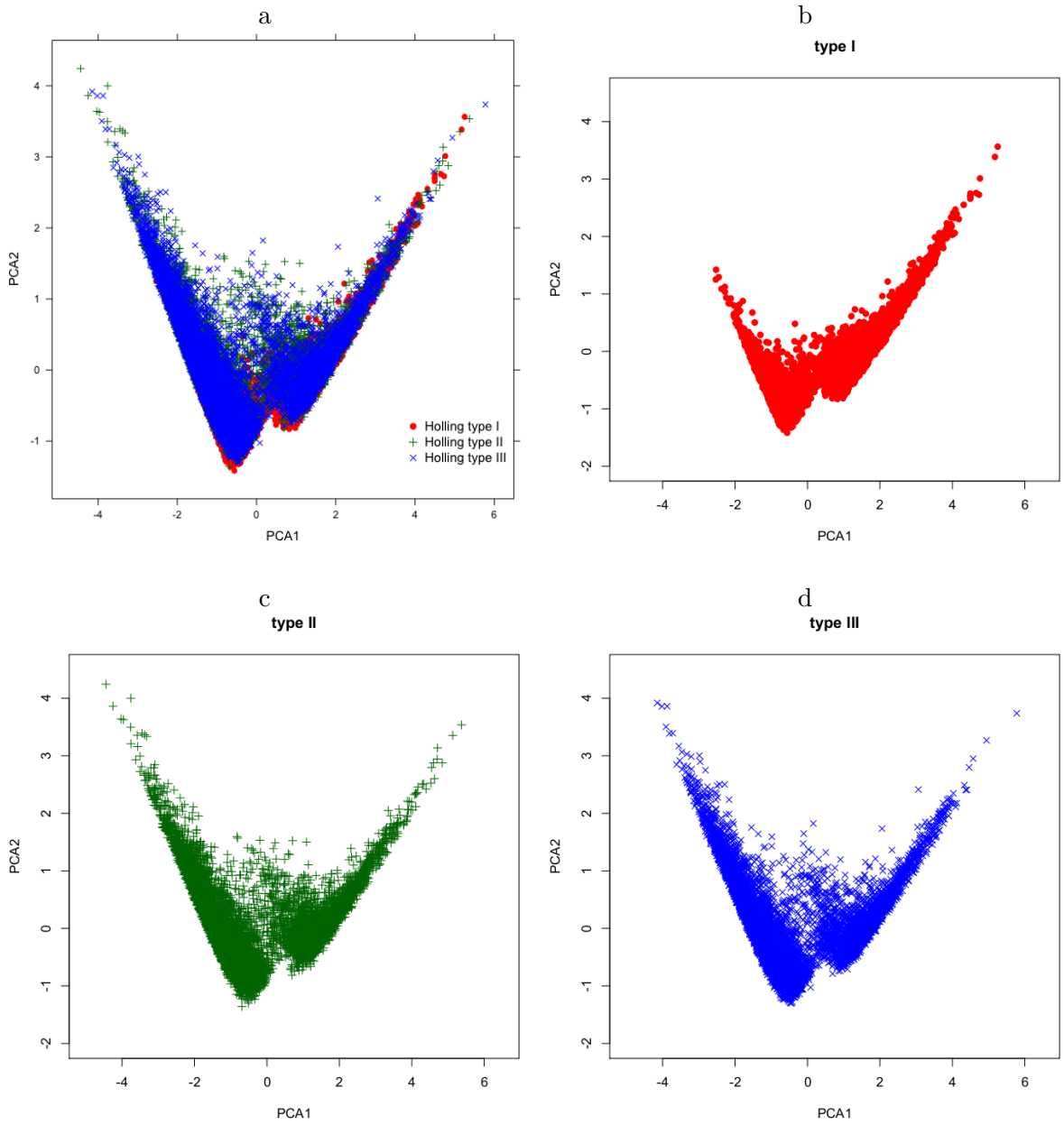


Figure 3.4: Effect of different formulation of lobster predation rate on the scores of simulation outcomes on the first two axes of the PCA, which capture 91% of the total variance. Scores are plotted for all functional responses (a) then respectively for Holling Type I (b), II (c) and III (d) functional responses. MANOVA Pillai's Trace statistic suggests a significant effect ($F_{2,23997} = 724.16$) of the functional response on simulation outcomes but this is likely to occur due to the very large number of replicates (8000 simulations for each response).

3.3.5 Types of simulations and key outputs screened for sensitivity analysis

Sensitivity analysis is key to test the robustness of a model and to assess the utility of its application in simulating ecological features of interest. In the case of TRITON, we used sensitivity analysis to dissect the influence of the different input parameters on the model's ability to shift from seaweed bed to sea urchin barren and back. Two main types of sensitivity tests were conducted: (1) we investigated the general behaviour of TRITON with a global sensitivity test in which all parameters varied and initial conditions were unconstrained for all three groups; and then (2) focused on the 'forward' (kelp bed to urchin barren state) and 'backward' (seaweed recovery from the barren state) shifts. In each of these cases, initial conditions were constrained to mimic either an urchin-free seaweed bed or, alternatively, a well-established sea urchin population on barren habitat. Model outputs were saved monthly for each 50-year-long simulation, and the extended FAST applied to several output metrics. The first of these was the simulated biomass of each model group. Note that the relative biomass of the seaweed bed is directly convertible to percentage cover of seaweed (or alternatively, percentage cover of reef that is barren habitat). We used the first axis of a Principal Component Analysis on the three normalised biomass densities as a one-dimensional summary of community state (accounting for 77% of the total variance). For simulations focusing on the 'forward' and 'backward' shifts, we additionally measured the time for the community to shift to the alternative state as an important feature of model dynamics. In the model, the barren state was defined as seaweed bed cover dropping under 10%, while the seaweed bed state corresponded to more than 75% of seaweed cover (see Fig. 3.5). All figures were produced in R and surface plots rely on the 'Krig' function of the 'fields' package (R Development Core Team, 2010).

3.4 Results

3.4.1 Calibration and validation of TRITON

At a holistic level, the capacity of the model to demonstrate shifts (in either direction) between seaweed- and sea urchin dominated reefs represents a validation of the observed dynamics. First, parameters of influence on model dynamics can provide the most effective means to calibrate model behaviour accordingly to observations: sensitivity analysis with the first set of Monte-Carlo simulations, initialised in the seaweed bed state and run under

historical fishing levels for the east coast of Tasmania, reveal that urchin and lobster recruitment rates are the most influential parameters on the model's ability to shift to sea urchin barrens (Fig. 3.2a). Moreover, the relationship between the two variables in affecting the risk of barren habitat formation is non-linear (Fig. 3.2b); for a given level of sea urchin recruitment, with declining annual lobster recruitment (from 800 g.200 m^{-2}.$year^{-1}$) there is initially little affect on the likelihood of barrens formation until a threshold of 600 g.200 m^{-2}.$year^{-1}$ is reached, at which point risk of barrens increases linearly with declining lobster recruitment to 400 g.200 m^{-2}.$year^{-1}$, below which there is little further affect on the likelihood of barrens forming. The smallest value of mean sea urchin recruitment rate that can achieve levels of barrens formation (∼50% of reef area) observed in NSW (Andrew and O'Neill, 2000) and Tasmania (Johnson et al., 2005, 2011) in areas where *C. rodgersii* is long established (i.e. the point at which the chance of barrens formation is 0.5; Fig. 3.2b) is 5000 g.200 m^{-2}.$year^{-1}$.). Consequently, sea urchin recruitment rates are varied between 5000 and 10000 g.200 m^{-2}.$year^{-1}$ in sensitivity tests presented in the rest of this paper.

Demonstrating the minor influence of the formulation of density dependence in lobsters' predation on urchins also contributes to model validation. The second set of sensitivity tests investigated the effects of alternative formulations of lobster predation on sea urchins, i.e. of implementing Holling's type I, II or III functional response. FAST sensitivity indices were computed for all parameters in TRITON under each formulation of the functional response, i.e. including the two parameters that define the shape of the functional response (Fig. 3.3). For each of the three formulations (i.e. Holling's type I, II or III), the two parameters defining the shape of the functional response had no more influence on model behaviour than did most of the other 14 input factors. Indeed, the influence of the two parameters of the functional response was marginal compared to those parameters with greatest influence on model behaviour (i.e. lobster fishing mortality, initial urchin population, lobster recruitment, initial seaweed cover, sea urchin recruitment). The projection of simulation outcomes on the first two PCs also suggests that the type of functional response adopted has marginal influence on model behaviour (Fig. 3.4). The patterns of the scores on the first two PCs, which capture 91% of the total variability, are visually very similar for all three functional responses. While scores on the first two PCs with the Holling Type I response (Fig. 3.3b) show a slightly different distribution compared to the Type II and III, the overall patterns are virtually similar. Note, however,

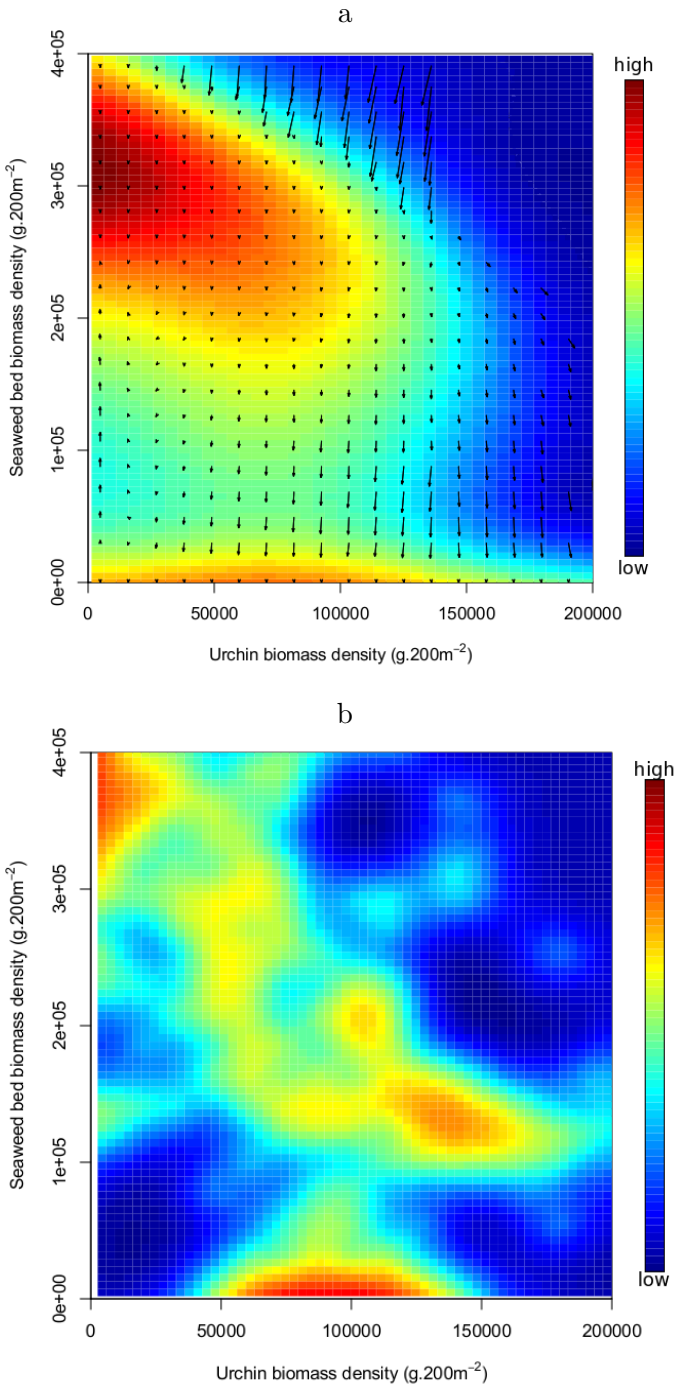


Figure 3.5: Frequency (logarithmic scale) of community states as a function of sea urchin versus seaweed bed biomass densities from (a) the 8000 Monte-Carlo simulations with TRITON and from (b) large-scale surveys on the east coast of Tasmania (Johnson et al., 2005, 2011). Arrows in (a) represent the mean simulation trajectory in terms of fortnightly change in sea urchin and seaweed bed biomass densities.

that results from the MANOVA suggest significantly different mean scores on the first two PCs for each Holling Type functional response, but this is likely to occur due to the very large number of replication (8000 simulations) bringing the multivariate standard errors to marginal values. Given that the model wasn't sensitive to the particular choice of functional response or to the parameterisation of this response, we chose to use Holling's type III functional response in all of the following simulations given that it is the most commonly used response to describe predation behaviour in decapods (see Table A.8; Appendix A).

We aggregated monthly outputs from the 8000 Monte-Carlo simulations of the FAST global sensitivity analysis with random initial conditions to compare patterns emerging from simulations with TRITON to patterns observed in large-scale surveys (Johnson et al., 2005, 2011) of Tasmanian temperate reef communities (Fig. 3.5). Fig. 3.5a describes the frequency of the different community states in terms of seaweed bed versus sea urchin biomass densities with overlayed arrows representing the model mean trajectory (i.e. fortnightly change in biomass through simulations) at different points of reef state. In Fig. 3.5b, data from a large-scale survey (Johnson et al., 2005, 2011) describes the frequency of reef communities on the east coast of Tasmania in 2000-2002 being in any given state. Importantly, both the modelled and observed reef communities identify two dominant states representing (i) the seaweed bed state with a high cover of seaweed and a low density of sea urchin and (ii) the sea urchin barren state with virtually no algal cover and a high density of sea urchins. This indicates broad agreement of the behaviour of the model with observations of the occurrence of the two states in the field.

3.4.2 Sensitivity analysis and parameters of influence on model behaviour

The sensitivity to input parameters of final abundances (after 50 years of community development) of seaweed, sea urchins and lobsters, and of overall community structure, was examined across 8000 Monte-Carlo simulations with unconstrained initial conditions (Fig. 3.6 and 3.7). Total extended FAST sensitivity indices quantify input parameters' relative contribution to model output variance for a given sensitivity test, but note that their absolute values are not comparable for different extended FAST tests. Overall, a similar suite of the most influential variables were identified for each component of community structure, namely fishing mortality of lobsters, lobster recruitment and recruitment rates

and initial abundances of sea urchins, although other variables were also influential. However, the rank order of influence differed depending on whether it was final densities of seaweed, sea urchins or lobsters that were examined. Final biomass density of seaweed is predominantly determined by, in order of importance: the initial density of sea urchins; lobster fishing mortality; seaweed growth rate; seaweed initial condition; and urchin recruitment (Fig. 3.6a). The five most influential parameters on final sea urchin biomass densities are lobster fishing mortality, sea urchin and lobster recruitment rates, as well as the two coefficients of Holling's type III functional response defining lobster predation rate (Fig. 3.6b). The final biomass density of lobsters is mostly determined by: lobster fishing mortality; recruitment rate; and sea urchin initial conditions (Fig. 3.7a). In comparison, other input parameters defining lobster population dynamics (e.g. initial condition, natural mortality, dependency to the state of the seaweed bed) have a lesser influence. Given these results, it is not surprising that overall community structure described by the first principal component of the mean-centred normalised simulated biomasses of the three groups (and accounting for 77% of the total variance; Fig. 3.7b) is most influenced by, in order of importance: lobster fishing mortality; initial sea urchin abundance; lobster and sea urchin recruitment rates; the two parameters defining lobster predation; and finally seaweed growth rate. Across all four outputs considered in this sensitivity analysis, the initial abundance, carrying capacity and recruitment rates of the seaweed assemblage; sea urchin natural mortality and their grazing rate; initial abundances and, natural mortality of lobsters, and the coefficient of lobster dependency on the state of the seaweed bed; and the parameter defining size-structured predation of lobsters on sea urchins have relatively marginal influences on the end point community structure in the simulations.

The final two sets of Monte-Carlo simulations quantify the contribution of input parameters to two specific and important features of model behaviour, respectively, the 'forward' shift from the seaweed assemblage to sea urchin barren habitat (Fig. 3.8), and the reverse ('backward') shift from sea urchin barrens to recovery of dense seaweed cover (Fig. 3.9). We conducted these sensitivity analyses on the scores of the first principal component of the mean-centred normalised simulated biomasses of the three model groups, as a one-dimensional summary of final community state (which explained 77% of the total variance in final community composition). Lobster recruitment rate, lobster fishing mortality, sea urchin recruitment rate and the two parameters defining lobster predation rate were the five most influential parameters on model's ability to shift from dense seaweed

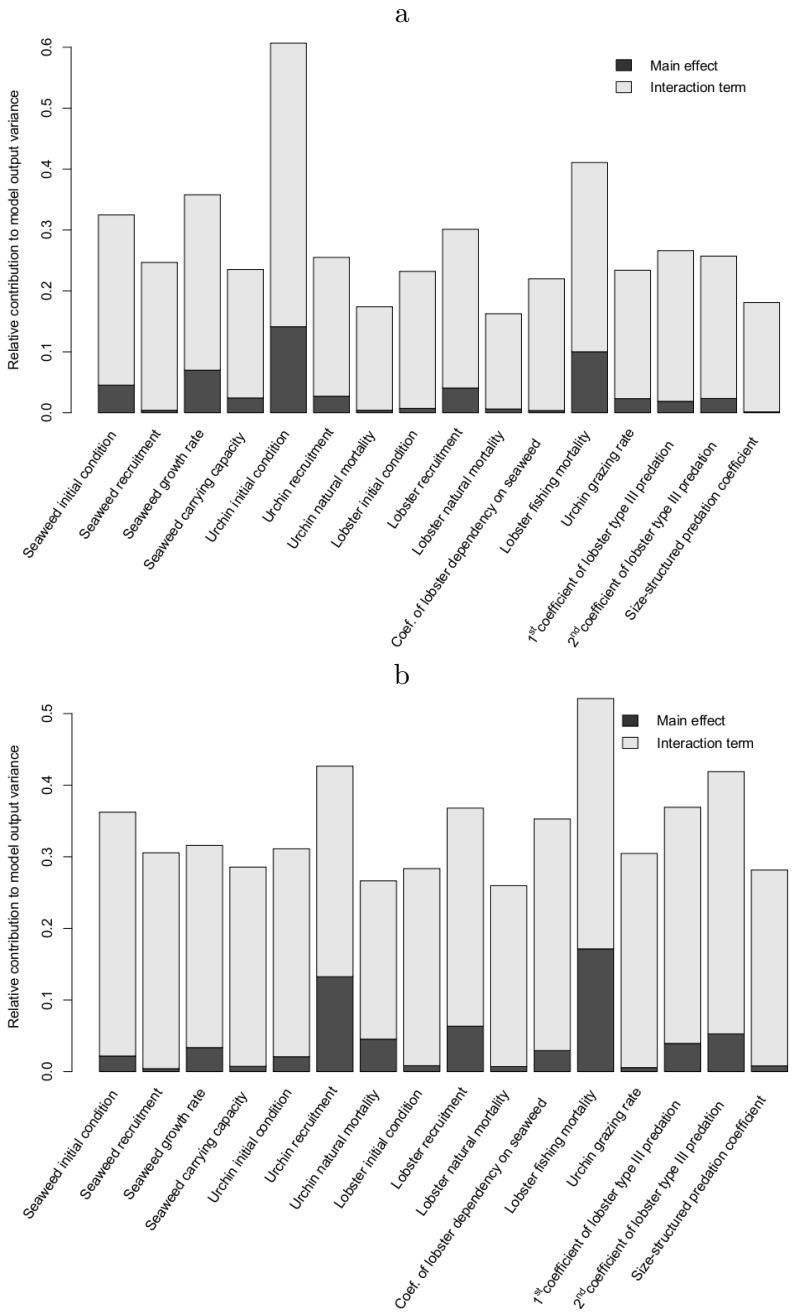


Figure 3.6: Sensitivity analysis based on extended FAST indices quantifying the contribution of all model input parameter values to model output variance. Final biomass densities of (a) seaweeds, (b) sea urchins at the end of 50-year simulations with unconstrained initial conditions are used as model outputs.

assemblage to sea urchin barrens (Fig. 3.8 a). TRITON's ability to shift from a sea urchin barren back to dense seaweed cover was essentially influenced by the values of lobster fishing mortality and recruitment rates, as well as sea urchin recruitment levels and the

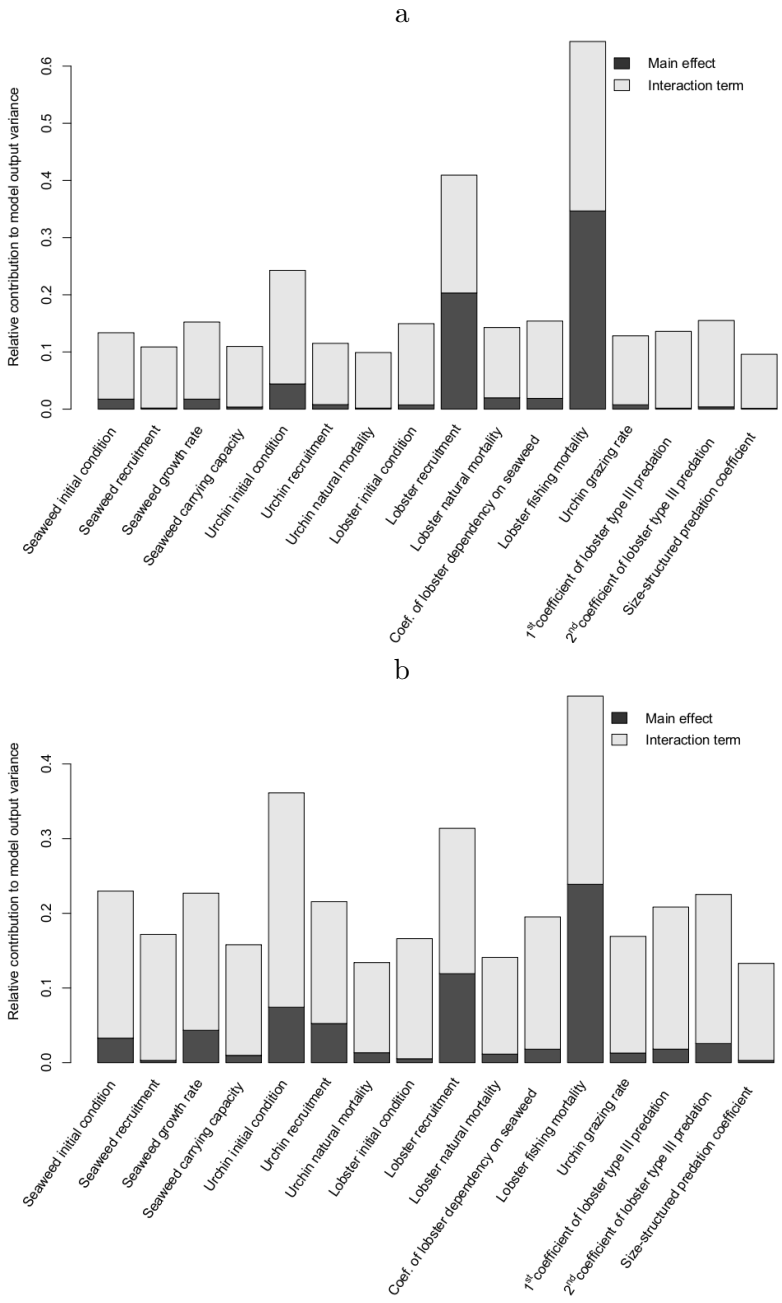


Figure 3.7: Sensitivity analysis based on extended FAST indices quantifying the contribution of all model input parameter values to model output variance. Final biomass densities of (a) rock lobsters) at the end of 50-year simulations with unconstrained initial conditions are used as model outputs. Additionally we considered the sensitivity of input parameters to final overall community structure described by the first principal component (PC1) from PCA on mean-centred normalised biomass density outputs across all three model groups (b).

dependency of lobster recruitment on the state of the seaweed cover (Fig. 3.9 a). Seaweed recruitment rate and the second coefficient of Holling's type III functional response, which determines the position of the plateau in the functional response (i.e. maximum predation rate), were also quite influential on model's ability to realise recovery of seaweed cover on (initially) barren habitat. Additionally, we considered the subset of simulations that respectively shifted 'forward' (Fig. 3.8 b), and 'backward' (Fig. 3.9 b), to investigate the effects of the two most influential parameters (lobster fishing mortality and mean lobster recruitment rate) on transition times for the modelled community to shift from its initial state to the other. For linear increases in lobster fishing mortality and decreases in lobster recruitment, the time to destruction of seaweeds and development of extensive sea urchin barren habitat becomes shorter in an essentially linear manner (Fig. 3.8b). Conversely, as fishing mortality on lobsters decreases and their recruitment increases, the time to recovery of seaweed cover from the barren state decreases in an approximately linear fashion (Fig. 3.9b). A final important point to emerge for all sensitivity analyses (Fig. 3.6-3.9) is that interaction terms contribute consistently more - and in most cases very much more - to the variance of model outputs than first order 'main' effects due to single input parameters acting directly on their own.

3.5 Discussion

3.5.1 Pattern-oriented model validation

Validation and calibration of the TRITON model, which captures alternative community states in Tasmanian seaweed-sea urchin-rock lobster dynamics, is one of the main objectives of this paper. Mean observed community state, commonly used as an objective to calibrate complex ecosystem models (e.g. Marzloff et al., 2009), is not a reliable or meaningful criterion to assess the realism of a model in which arises alternative community states. In addition, the set of difference equations comprising the TRITON model are not analytically tractable to identify the parameter space in which the model shifts discontinuously from the seaweed-dominated state to the sea urchin barren state and back as has been possible for models of coral reef community dynamics with hysteresis (see Fung et al., 2011). Thus, calibration and validation of TRITON relies on two large-scale features that emerge from the dynamics of rocky reef communities under the threat of *C. rodgersii* destructive grazing. First, following the long-term establishment of *C. rodgersii*

in regions where key urchin predators are ostensibly at relatively low abundances, about 50% of inshore rocky reef habitat occurs as extensive *C. rodgersii* barren habitat (Andrew and O'Neill, 2000; Johnson et al., 2005). We restricted mean recruitment rate for *C. rodgersii* to allow for the model to both simulate realistic biomass densities of sea urchins on barren habitat, and to realise the shift from seaweed bed to sea urchin barren with a probability of 0.5 under depletion of large lobsters by fishing (Fig. 3.2). Second, intensive surveys of seaweed cover and barren habitats along the east and southeastern coasts of Tasmania, including quantifying densities of sea urchins and other reef species, provided a benchmark of the range and frequency of community states observed on the east coast of Tasmania (Johnson et al., 2005). The ability of TRITON to reproduce these large-scale patterns, showing the two main community states of high seaweed bed with low sea urchin abundance or sea urchin barren habitat with virtually no macroalgal cover (Fig. 3.5), is a useful validation of the model.

The capacity to investigate mean simulation trajectories (Fig. 3.5b) illustrates the value of TRITON to explore features of reef community dynamics that are challenging (or impossible) to observe or measure in any detail or with sufficient precision in the field (e.g. the existence of thresholds points leading to shifts in community state). It is an important result that the model demonstrates an ecological hysteresis (Scheffer and Carpenter, 2003; Donahue et al., 2011) in model dynamics, showing two stable community states (i.e. the zones where simulation trajectories converge), and an unstable equilibrium zone, where the trajectories diverge, developing towards one state or the other (Fig. 3.5b). The mean simulation trajectories confirm the occurrence of two alternative community states sensu Petraitis and Dudgeon (2004) such that under identical environmental conditions, initial conditions determine whether the simulated community develops to the sea urchin barren or seaweed-dominated state. We conclude that pattern-oriented modelling, originally proposed to validate agent-based model (Grimm et al., 2005), can provide a valuable approach for a simulation-based assessment of the dynamics of ecological models that manifest alternative community states.

3.5.2 Model sensitivity to input parameters

Breaking down the sensitivity analysis into a series of tests screening for different model outputs and different aspects of model behaviour (i.e. 'forward' and 'backward' shifts)

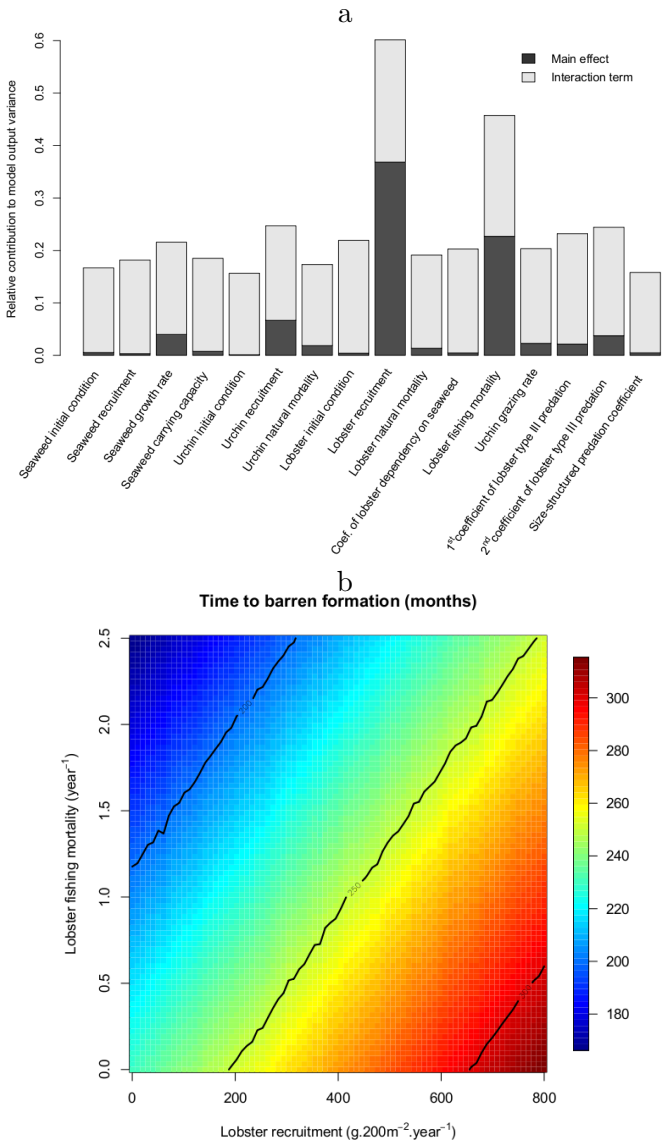


Figure 3.8: Sensitivity of the 'forward' shift, from high seaweed biomass to sea urchin barren habitat, to model input parameters (i.e. this analysis was restricted to those simulations in which the 'forward' shift occurred). Initial conditions correspond to the seaweed bed state with seaweed cover at >50% of carrying capacity, low initial sea urchin density (< 40000 g. 200 m^{-2}) and random rock lobster biomass density. a) Extended FAST indices quantifying the contribution of input parameter values to model output variance in overall community structure (described as the first PC from the PCA on mean-centred normalised biomass density outputs of all groups) for 50-year simulations. b) Time to barrens establishment (in months) as a function of the two parameters most influential in affecting the likelihood of the transition to barrens, *viz.* lobster recruitment rate and lobster fishing mortality.

is a means to robustly identify input parameters that have a consistently small or large influence on simulation outcome (Klepper, 1997). Overall, the identity of variables most influential in accounting for variance in simulation outcomes is similar across the different types of sensitivity tests we conducted (unconstrained initial conditions, or a constrained focus on the 'forward' or 'backward' shift), and whether we considered final abundances of individual groups (seaweed, sea urchins and lobsters) or of the community as a whole (Fig. 3.6, 3.7, 3.8 and 3.9). These analyses identified, lobster fishing mortality, lobster and urchin recruitment rates, as well as initial densities of the sea urchin as the key drivers of model dynamics. Conversely, seaweed recruitment rates, initial cover and carrying capacity (i.e. upper limit of seaweed biomass density); sea urchin natural mortality and grazing rate; and the initial biomass and natural mortality rates of rock lobster and the parameter defining size-structured predation of lobster on urchin, all have relatively marginal influence on the simulation outcomes.

At a more detailed level, the independent sensitivity tests were useful to identify differences in the key variables influencing the different individual components of community structure, and in comparing the influence of each input variable on particular groups (seaweed, sea urchins or lobsters) with the influence on overall community structure (as described by the first principal component from the PCA). While input parameters that most influence model dynamics are broadly similar for each component of the community, the detailed differences between these four different tests (Fig. 3.5) are informative:

(i) Seaweed biomass density is the only component for which dynamics is driven primarily by the initial state of the sea urchin population rather than lobster fishing mortality. This occurs as a result of the hysteresis in model dynamics with initial sea urchin biomass density sitting either higher or lower than the threshold above which the seaweed bed gets depleted by grazing (cf. Fig. 3.5b). Note that seaweed growth rate also exerts relatively high influence on seaweed dynamics, suggesting that rocky reefs where seaweed productivity is low (due to shading, unsuitable substrate or nutrient-poor conditions) will be more prone to sea urchin barren formation for the same level of sea urchins. Declining nitrate availability as a result of a changing ocean climate increasingly influenced by nitrate-poor waters of the East Australian Current (Johnson et al., 2011) may play a key role in this context.

(ii) Sea urchin dynamics in the model is essentially affected by input factors related to lobster predation pressure (the recruitment rate of lobsters, fishing mortality and the coefficients of Holling Type III functional response), as well as recruitment rates of the sea urchins themselves. This implies that, at the scale of an individual rocky reef, exposure to large-scale oceanographic features transporting urchin larvae (Banks et al., 2007), the suitability of the reef substrate (e.g. appropriate settlement cues, complexity of crevice structure; Andrew (1993)) for urchin metamorphosing larvae and settlement, or exposure to predation (Ling and Johnson, In press) can locally limit the potential for the *C. rodgersii* population to develop. Of all of these variables, clearly lobster fishing mortality is the key feature amenable to ready management intervention.

(iii) The rock lobster population is influenced largely by fishing and the mean recruitment rate to the population in the model. To a lesser extent lobster biomass density is also influenced by the initial biomass of sea urchins and the strength of the dependency of lobster recruitment on macroalgal cover. These latter two factors relate directly to the reduced potential for local lobster recruitment once extensive sea urchin barren habitat forms.

(iv) Not surprisingly, sensitivity indices focussed on effects on the variance in overall community structure (as described by the first principal component) identify all the parameters important to each of the three components of community structure when they are examined separately (Fig. 3.6 and 3.7a).

Conducting independent sensitivity tests to dissect model sensitivity in the 'forward' and 'backward' shifts separately (Fig. 3.8 and 3.9) was also very useful. This approach overcomes concerns about sensitivity analyses of models with multiple equilibria (van Nes and Scheffer, 2003). It identified that model shifts from high seaweed cover to sea urchin barren habitat, and the reverse shift realising recovery of seaweeds, are both driven predominantly by lobster fishing mortality, lobster and sea urchin recruitment rates, as well as lobster predation rates. Note however, that the reverse shift is also sensitive to the coefficient that scales lobster recruitment to the level of canopy cover; a strong dependency of lobster recruitment on the seaweed canopy creates a strong positive feedback between seaweeds, urchins and lobsters once the macroalgal canopy is lost, which contributes to

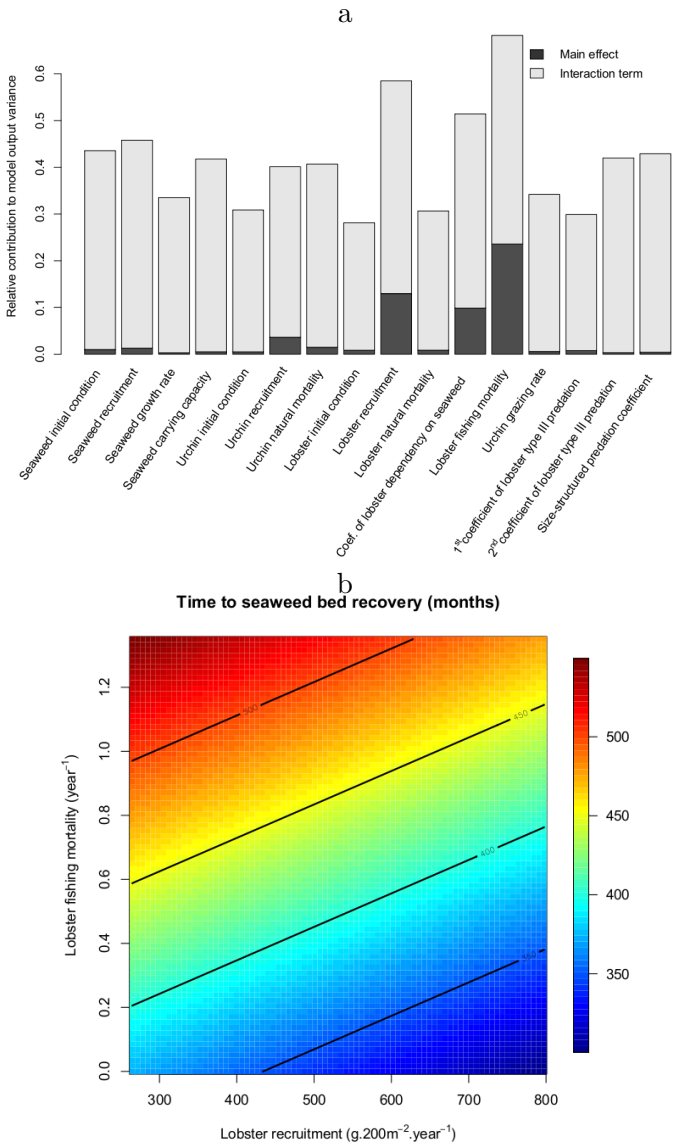


Figure 3.9: Sensitivity of the 'backward' reverse shift, from sea urchin barrens to recovery of dense back to seaweed bed state, to model input parameters (i.e. this analysis was restricted to those simulations in which the 'backward' shift occurred). Initial conditions correspond to sea urchin barren habitat, with seaweed cover <10% of carrying capacity, initial urchin density > 70000 g. 200 m^{-2} and random rock lobster biomass density. a) Extended FAST indices quantifying the contribution of input parameters to model output variance in overall community structure (described as the first PC from the PCA on mean-centred normalised biomass density outputs of all groups) for 50-year simulations. b) Time to recovery of seaweed cover (in months) as a function of the two most influential parameters influencing this transition, *viz.* lobster recruitment rate and lobster fishing mortality.

the high resilience of the urchin barren state (Marzloff et al., 2011*a*). Parameters of high influence identify the key ecological processes that drive community dynamics in the model. Given that the emergent dynamics of the model broadly matches observations of community state on eastern Tasmania reefs (Fig. 3.5), we can have some confidence that sensitivity analysis of TRITON helps to identify the likely key drivers of the dynamics in nature, and thus assists with both prioritising ongoing work in the field and in identifying options for improved management of Tasmanian reef community dynamics.

Transition times in shifting from one state to the other are important characteristics of the dynamics of systems with alternative states. Thus, transition times are a key element in exploring model sensitivity (Fig. 3.8b and 3.9b). For models with hysteresis, simulation outcomes are essentially binary, which can prove problematic when conducting sensitivity analyses, in particular in undertaking partial sensitivity tests to one input parameter at a time (van Nes and Scheffer, 2003, 2004). In the case of TRITON, the simulated community ultimately moves either towards the barren or the seaweed-dominated state (Fig. 3.5), and so quantifying the influence of parameters on the time for the model to shift 'forward' from seaweed bed to sea urchin barrens, or 'backward' to effect seaweed recovery, provides valuable insight into the detailed dynamics. Notably, the 'forward' shift (18.7 years +/- 0.17 standard error) occurs on average about ten years more quickly than the 'backward' shift (28.8 +/- 1.08 standard error). These mean transition times, which provide another illustration of hysteresis in model dynamics in the sense that 'forward' and 'backward' shifts are independent dynamics with different transition times, have very strong implications for management of rocky reef communities in Tasmania. Preventing the further spread of extensive sea urchin barrens appears as the only realistic and time-efficient management option. With no human interventions currently available to directly deplete the sea urchin population at an appropriate scale, the time frame for restoration of the original seaweed bed state from *C. rodgersii* barrens is of the order of three decades under the most drastic measures for the lobster fishery (Fig. 3.9 b). This exceeds by far the time span of current management plans for the Tasmanian lobster fishery.

The sensitivity analysis highlights that interactions between input parameters, rather than direct linear effects, have a major influence on simulation outcomes. The dominant influence on model behaviour of these interactions between input parameters is common in model of complex dynamics (Saltelli et al., 1999, 2009). In the context of the dynamics

of Tasmanian rocky reef, strong interactions between input parameters highlight the value of ecological models to inform managers of natural resources about non-trivial effects of management interventions and environmental changes on ecosystem state. While qualitative modelling can track the influence of indirect effects and the contribution of high level feedback to community dynamics (Marzloff et al., 2011*a*), simulation-based sensitivity analysis suggests that the quantitative model TRITON captures non-trivial interactions between modelled processes and can provide some valuable insights about indirect responses of reef community to perturbations or management interventions.

3.5.3 Model limitations and guidance for future research

Derivation of all parameter estimates was based upon the best available information (see Appendix A for further details). However, the results presented here are only as useful as the precision and accuracy of the parameter estimates, and so it is worthwhile acknowledging areas where parameter definition or the relative coarseness in representing ecological processes may limit the realism of TRITON. The last section of Appendix A lists some of the ecological processes of seaweed-urchin-lobster dynamics on subtidal rocky reefs around Tasmania that are captured rather coarsely in TRITON, and which would benefit from further field-based research. In particular it would be useful to have quantitative estimates of the effects of storm and wave action on seaweed cover (e.g. Reed et al., 2011); size-dependent vulnerability of macroalgae to grazers and the magnitude of any size-structured dynamics of seaweed beds; density-dependence in sea urchin grazing rate; importance of seaweed habitat to the recruitment, productivity and carrying capacity of lobster population; lobster predation rates at medium and high sea urchin densities (i.e. density dependence in predation impact); and effects of habitat, depth and reef profile on all of the modelled processes. If any of these effects is large, then the detail of model dynamics may be different to that presented here. However, it is unlikely that any of these effects would materially influence the qualitative dynamics of the phase shifts and hysteresis in broad terms.

3.6 Conclusions

Communities with the potential for multiple stable states and ecological hysteresis offer high stakes particular challenges for managers because one of the alternative states is

usually poorly productive and less desirable (Johnson and Mann, 1988; van de Koppel et al., 1997; Lawrence et al., 2007; Melbourne-Thomas et al., 2011*b*; Strain and Johnson, In press). It thus becomes of critical importance to avoid transition to that state, not the least reason for which is that it can be impractical for management intervention to effect the return shift. In this context, and particularly because it is not usually possible to identify tipping points from field based exercises (Hastings and Wysham, 2010; Osman et al., 2010; but see Carpenter et al. (2011) for a quite unique "whole-ecosystem" experiment), models of ecological communities with alternative states are essential to inform key thresholds in system dynamics and test the effects of alternative management strategies (Mumby et al., 2007; McClanahan et al., 2011). However, validating this kind of model remains challenging. Here we present a comprehensive simulation-based exploration of the TRITON model that captures the potential for Tasmanian seaweed-sea urchin-lobster community dynamics to shift between two alternative states, dense seaweed bed or sea urchin barren habitat. The series of Monte-Carlo simulations depicted the model's overall behaviour and Pattern-oriented-modelling, i.e. comparison of patterns emerging from simulations to large-scale patterns observed in the field, provided an efficient way to assess the robustness and realism of broad TRITON dynamics. The extended FAST routine (Saltelli et al., 1999), available within R's *sensitivity* package, provides a unique, computationally efficient framework to design robust model-independent sensitivity tests. Using the extended FAST, we identified parameters of influence to overall model dynamics, as well as to independent features of model hysteresis, i.e. 'forward' and 'backward' shifts between the two alternative community states. This enabled assessment of whether management intervention in this system is practicable, and to identify the nature of the intervention that is likely to have most effect in influencing community dynamics. Of the relatively small suite of parameters to which the model is most sensitive, fishing mortality of lobsters emerges as the single factor to which the model is particularly sensitive and on which human behaviour has a large and direct effect.

3.7 Acknowledgments

If this modelling work only captures a coarse version of Tasmanian rocky- reef local dynamics, it would merely have no groundings into reality at all without all the data referred to in this document: experimental studies (e.g. Ling et al., 2009*a*); empirical observations (e.g. Johnson et al., 2005); or monitoring of community recovery following

protection from fishing (e.g. Barrett et al., 2007). We would like to thank Neville Barrett, Graham Edgar and collaborators for generously sharing their 20-year-long dataset of monitoring reef community responses following protection from fishing; Klaas Hartmann and Caleb Gardner for informing some of parameters defining rock lobster dynamics; Kevin Redd for sharing the DNA-based estimates of lobster predation; Malcolm Haddon for useful discussions about size-structured modelling and recruitment stochasticity; Pip Bricher, the Mount family and Bruny for the writing retreat.

Chapter 4 Alternative states on Tasmanian rocky reefs: Identifying thresholds in community dynamics and assessing management interventions to limit destructive grazing of sea urchins

4.1 Abstract

Like many shallow temperate marine systems worldwide, Tasmanian inshore rocky reefs can occur in alternative persistent community states. The shift from dense productive seaweed beds to sea urchin 'barrens' habitat, i.e. largely bare rock following the destructive grazing of macroalgal cover and sessile invertebrates by sea urchins, significantly affects ecosystem structure and functioning and has major implications for the management of rocky reef communities. Along with dramatic loss of habitat and species diversity, the establishment of extensive barren habitat constitutes an immediate threat to the productivity of Tasmanian fisheries. The transition to barren habitat, however, can be swift and is difficult to study empirically. In particular, knowledge about key thresholds in community dynamics, which provide reference points for sound management of the system, and an assessment of the effectiveness of possible management levers to mitigate the ecological impacts of sea urchin grazing are lacking.

Through Monte-Carlo simulations with a model of the eastern Tasmanian rocky reef community that realistically captures (i) the potential for both 'forward' shifts from dense seaweed beds to sea urchin barrens and 'backward' shifts from barren habitat to seaweed recovery, and (ii) the associated hysteresis, we identify thresholds in community dynamics and test the effectiveness of alternative management options both in terms of mitigating the ecological effects of sea urchin destructive grazing, and performance of the lobster fishery. Differences in the threshold for 'forward' and 'backward' shifts reflect a hysteresis in reef dynamics, i.e. once sea urchin barrens form extensively,

restoration of dense seaweed beds becomes much more difficult to achieve than prevention of barren habitat formation in the first place. The risk of barrens formation increases significantly with lobster fishing mortality. The modelling suggests that direct culling of sea urchin populations combined with a reduction in lobster fishing pressure is likely to be more effective in terms of ecological outcomes and improved fishery performance, than intervention aimed only at rebuilding lobster populations to control urchin density through predation. The model simulations highlight the need for the Tasmanian rock lobster fishery management objectives to move away from a single-species orientation focussing on maximum sustainable yield towards a more conservative ecologically sustainable yield that accounts for the ecosystem services delivered by rock lobster to rocky reef communities.

4.2 Introduction

Variability is a key characteristic of ecological dynamics (Doak et al., 2008). In some ecological systems, in addition to relatively short-term space-time variability in dynamics (e.g. seasonal, interannual), environmental or anthropogenic perturbations can facilitate sudden shifts between alternative persistent community states (May, 1977; Scheffer et al., 2001; Beisner et al., 2003; Scheffer and Carpenter, 2003). These abrupt changes in community dynamics can dramatically alter ecosystem functioning and have disastrous consequences for the human activities that rely on them. These phase shifts are challenging to anticipate and their consequences difficult to predict (Doak et al., 2008), so that systems with the potential for these shifts represent particular challenges for ecologists and managers alike (Sutherland et al., 2009).

Phase shifts are often swift and are usually observed *a posteriori*, i.e. once the community has shifted to the alternative state. Hence, thresholds in the dynamics of marine ecosystems with alternative persistent states are notoriously difficult to identify empirically (de Young et al., 2008; Doak et al., 2008; Hastings and Wysham, 2010). Additionally, experimental assessment of the effects of alternative management scenarios on community state is hardly ever achievable in marine ecosystems at an appropriate scale. For these reasons, and because the triggers and behaviours of phase shifts are unique to each ecosystem, tailored case-specific simulation models represent a valuable tool to explore ecological dynamics with alternative community states, test the effects of management scenarios and inform decision making for particular circumstances (Scheffer and Carpenter,

2003; de Young et al., 2008). Several ecological models developed to capture the essential dynamics of marine ecosystems with alternative community states have been developed over the last decade, and include some designed explicitly for application in management support (see Mumby et al., 2007; Melbourne-Thomas et al., 2010 for some coral reef examples).

We developed a model, called TRITON (for Temperate Reefs In Tasmania with lObsters and urchiNs), of the dynamics of seaweed-based reef communities in eastern Tasmania (Chapter 3). In this region, shallow ($<$ 35 m depth) exposed rocky reef communities essentially occur in one of two alternative persistent states: (1) as a dense cover of macroalgae; or (2) as sea urchin 'barrens' habitat characterised by a poorly productive and largely bare rock habitat following destructive grazing of the seaweeds and sessile benthic invertebrates by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of these widespread sea urchin barrens results from the combined effects of climate-driven range extension of the sea urchin from Australia's mainland to Tasmania via strengthening eddy activity of the tropical East Australian Current (Ling et al., 2009*b*) and depletion of biomass of large southern rock lobster (*Jasus edwardsii*) as the only effective predator of the long-spined sea urchin in Tasmania (Ling et al., 2009*a*). Relative to the seaweed bed state, *C. rodgersii* barrens represent dramatic losses of habitat, species diversity and productivity, including commercial species such as blacklip abalone (*Haliotis rubra*) and southern rock lobster, the two most valuable fisheries in Tasmania (Ling, 2008). Thus, the spread of sea urchin barrens in eastern Tasmania has been identified as a major threat to the sustainability of the important lobster fishing industry (Johnson et al., 2005; Pecl et al., 2009).

In this paper, we address a range of key questions for the management of Tasmanian reef communities using Monte-Carlo simulations with the TRITON model:

(i) What are the characteristics thresholds in community dynamics? These tipping points, which cannot easily be directly observed empirically, provide essential reference points for management to minimise the risk of barren formation or facilitate the recovery of seaweed beds from the barren state;

(ii) What are the merits and overall effectiveness of alternative management scenarios to either prevent the establishment of sea urchin barren habitat, or restore dense seaweed

beds from sea urchin barrens? Here we test, both independently and conjointly, the effectiveness of available management levers: reducing lobster fishing, implementing a maximum legal catch size to protect large lobsters as key predators of the sea urchins, and culling of sea urchin populations and translocating large lobsters from deep to shallow reefs exposed to sea urchin destructive grazing.

(iii) How is the performance of the rock lobster fishery in eastern Tasmania, estimated from simulated catches with TRITON and overlain with a version of the current Tasmanian rock lobster stock assessment model, affected by different management scenarios? Over the last two decades, fisheries scientists have increasingly emphasised the need to account for the ecosystem effects of fishing, and to shift management practises away from a traditional single species focus towards an ecosystem-based approach (Smith et al., 2007, 2011). It is in this context that this question is addressed. With this simple example in which lobsters play an important ecological role as predators of sea urchins, we illustrate some of the misleading assumptions of single-species focus when the target species delivers key services to the ecosystem. We highlight the need for fishery management targets, such as maximum sustainable yield (MSY), to account for ecological services delivered by commercial species, and suggest that these targets may need to be revised to maintain ecosystem functioning. This will be particularly important for ecological systems in which the dynamics are characterised by alternative community states with hysteresis, i.e. where phase shifts are particularly difficult to reverse.

4.3 Material and Methods

We outline below (1) a concise description of the TRITON model; (2) characteristics of the simulations and model outputs presented in this paper; and (3) some specifics about the different sets of Monte-Carlo simulations designed to test the consequences of alternative management scenarios.

4.3.1 TRITON model of Tasmanian lobster-sea urchin-seaweed community dynamics.

The TRITON (Temperate Reef In Tasmania with lObsters and urchiNs) model provides a 'minimum-realistic' (Fulton et al., 2003*a*) representation of the dynamics of Tasmanian

inshore rocky reef communities with a specific focus on shifts in community structure from the seaweed-dominated to the sea urchin barrens state and back. Fishing of southern rock lobster, a key predator of sea urchins on Tasmanian inshore reefs, is the major anthropogenic activity affecting community state (Ling et al., 2009*a*). Thus, to focus on key management questions related to the establishment of *C. rodgersii* barrens on the East coast of Tasmania, TRITON only explicitly describes the dynamics of three functional groups or species: (1) the seaweed assemblage (e.g. *Phyllospora comosa*, *Ecklonia radiata* and a range of other canopy forming and understorey brown, red and green macroalgal species); (2) the long-spined sea urchin, *Centrostephanus rodgersii*; and (3) the southern rock lobster, *Jasus edwardsii*. Predation of lobsters on sea urchin is size-structured given that it is large individuals (carapace length >140 mm) that effect predation control on *C. rodgersii* (Ling et al., 2009*a*).

The mean field model realistically captures benthic dynamics at the scale of a patch of reef (area of 10^2-10^4 m^2) across the most common depth range of sea urchin activity, i.e. 8-35 m (Chapter 3). The default parameterisation corresponds to a 200 m^2 area of reef (Table 3.1) and uses the latest information available about the ecology of Tasmanian reef community. Model uncertainty has been tested comprehensively with regards to model structure (Marzloff et al., 2011*a*), formulation and parameterisation (Chapter 3). The difference equations capturing the dynamics of each functional group are detailed in Chapter 3. When referring to simulations with a simplified version of the single-species Tasmanian rock lobster stock assessment model, lobster population dynamics follows Eq. 4.1. Eq. 4.1 is similar to Eq. 3.3 capturing rock lobster dynamics in TRITON except that stochastic recruitment to the first size class is assumed lognormal and independent of both local biomass density of lobster (i.e. large-scale regional supply of larvae) and local

extent of sea urchin barren habitat.

$$RL_{s,t} = max\left(0, \underbrace{r_{CR}}_{\text{Recruitment to the first size class (Only if s = 1) unaffected by sea urchin barrens}} + \underbrace{\sum_{j=1}^{j<s}(\delta'_{s,j} \times RL_{j,i}) - (\sum_{i>s}^{N_{RL}} \delta_{i,s}) \times RL_{s,t}}_{\text{Growth between different size classes accounts for individual weight gain}} + \underbrace{RL_{s,t} \times exp(-\beta_{RL})}_{\text{Biomass at time t affected by natural mortality}} - \underbrace{RL_{s,t} \times (1 - exp(-F_{RLs}))}_{\text{Fishing mortality}}\right) \quad (4.1)$$

with $RL_{s,t}$ denotes the biomass of rock lobsters in size class s at time t (g. 200 m^{-2}); r_{RL}, lobster recruitment rate (g. $year^{-1}$. 200 m^{-2}) in which mean recruitment rate μ_{RL} varies stochastically following a lognormal stochastic function of mean 0 and standard deviation σ_{RL}; β_{RL}, lobster natural mortality ($year^{-1}$); $\delta'_{s,j}$, biomass-based transition probability from size class j to s, or element of the s^{th} row, j^{th} column of the transition probability matrix ($year^{-1}$ or g. g^{-1}. $year^{-1}$); $\delta_{i,s}$, abundance-based transition probability from size class s to i ($year^{-1}$ or individual.individual^{-1}.year^{-1}); SW_t, seaweed biomass (g. 200 m^{-2}); F_{RLs}, fishing mortality for lobster of class s ($year^{-1}$).

TRITON is implemented using the open-source object-oriented Python programming language version 2.6 with the 'numpy' and 'scipy' packages (Python Software Foundation, 2008). Discrete-time modelling was chosen for ease of implementation and computational efficiency. A two-week-long time step was adopted to prevent numerical instability and ensure consistency of model behaviour with results from continuous-time modelling using differential equations (Deng, 2008).

4.3.2 Simulation characteristics and model outputs (Table 4.1)

All results presented in this paper rely on two types of model outputs, viz. standing biomass density fresh weight ($g.200m^{-2}$) and annual catches as fresh weight, i.e. biomass loss due to fishing mortality ($g.200m^{-2}.year^{-1}$). For each 50-year-long simulation, model outputs were saved monthly. We adopted two different ways to explore tipping points in modelled reef dynamics:

(i) We first considered all monthly biomass outputs within each 50-year-long simulations

and used seaweed bed relative cover to characterise community state. This approach allowed to closely monitor model dynamics (every monthly time step) so as to precisely seize the critical thresholds at which, either the model shift from the seaweed-dominated state to sea urchin barren habitat (e.g. Fig. 4.2) or shift back to dense seaweed bed from established barrens (Fig. 4.4). For these analyses, we adopted 75% of seaweed cover as the threshold above which sea urchin grazing only has marginal effects on seaweed bed cover (See Fig. 3.5a displaying TRITON's mean trajectory through simulations).

(ii) We also adopted a more general approach to characterise thresholds in terms of long-term probability of model to shift across all simulations. When considering the long-term probability of barren habitat formation (e.g. Fig. 4.1 or 4.5) or seaweed bed restoration (e.g. Fig. 4.3 or 4.7) across simulations, we computed mean values of monthly outputs over the last 10 years of the simulation to minimise effects of interannual stochasticity. From Fig. 3.5a displaying TRITON's model dynamics, we can safely assume that the model has shifted from the seaweed bed to the barren state if seaweed bed relative cover is below 10% at the end of a simulation; For the reverse shift from sea urchin barrens (less than 10% of seaweed cover) to dense seaweed bed, successful recovery of the seaweed bed state can be assumed if seaweed cover is above 50% at the end of the simulation (cf. Table 4.1).

These tipping points were characterised in terms of standing biomass density of the following modelled groups: sea urchin, rock lobster and large size classes of rock lobster (carapace length $>$ 140 mm).

Table 4.1: Characteristics of the different sets of Monte-Carlo simulations: (a) initial conditions corresponding either to the seaweed bed, or to sea urchin barren habitat; (b) ranges of values for sea urchin fishing mortality, maximum legal catch size for lobsters, and the mean lobster recruitment rate associated with the different management scenarios.

a) Initial conditions for each of the two states (biomass densities in g. 200 m^{-2})

	Dense seaweed cover	**Sea urchin barrens**
Seaweed assemblage	$2 \times 10^5 - 4 \times 10^5$ (i.e. more than 50% cover)*	$0 - 4 \times 10^4$ (i.e. less than 10% cover)*
Sea urchins	$0 - 4000$ (i.e. less than 10% of carrying capacity on barren)	$7 \times 10^5 - 1.4 \times 10^5$ (i.e. more than 50% of carrying capacity on barren)
Rock lobsters	$0 - 1.4 \times 10^4$	$0 - 1.4 \times 10^4$

* The same values are used to define presence (1) or absence (0) of a shift to the alternative state at the end of a simulation: a persistent shift to sea urchin barrens is assumed if the seaweed bed drops below 10% cover, while recovery of seaweeds corresponds to the seaweed bed re-growing above a 50% of cover.

b) Simulation characteristics in terms of sea urchin culling or harvesting, maximum legal catch size for lobsters, and mean lobster recruitment rate. Lobster fishing mortality varies between 0 and 2.5 year^{-1}

	Sea urchin cull rate F_{CR} (year^{-1})	**Maximum legal size** F_{maxRL} (mm)	**Lobster recruitment rate** μRL (g.200 m^{-2}.year^{-1})
Range	0 - 2.5	135 - 165	200 - 800
Low	0 - 0.5	135 - 145	200 - 400
Moderate	0.5 - 1.5	145 - 155	400 - 600
High	1.5 - 2.5	155 - 165	600 - 800

Using R's generalised linear model (GLM) routine (R Development Core Team, 2010), we fitted logistic binomial models (Fig. 4.1, 4.2, 4.3 and 4.4) to relate seaweed cover or the probability of community shift (i.e. barren formation or restoration of the seaweed bed; Table 4.1) to the standing biomass density of different model groups. The binomial GLM routine estimates the coefficients α and β in: $log(\frac{p}{1-p}) = \alpha + \beta x$ where p is the predicted variable (probability of community shift, or seaweed relative cover expressed as the ratio of seaweed standing biomass density on seaweed carrying capacity) and x is the explanatory variable (standing biomass density of large lobsters, i.e. of carapace length >140 mm, or sea urchins). We use α and β to objectively characterise model thresholds as $x = \frac{log(\frac{p}{1-p})-\alpha}{\beta}$. Thresholds were defined as: the points where the risk of sea urchin barrens formation equals p = 5%; or the points where the probability of long term seaweed bed recovery equals p = 95%; or the points associated with p = 75% of seaweed cover as an adequate threshold above which the effect of *C. rodgersii* destructive grazing on the dense seaweed canopy is marginal (cf. Fig. 3.5a about mean trajectory through simulation).

The extended Fourier Amplitude Sensitivity Test (extended FAST; Saltelli et al., 1999), available within R's *sensitivity* package, was used to comprehensively explore parameter space and define the envelope around parameter uncertainty through Monte-Carlo simulations. Python package *Rpy2* provided an interface between Python (Python Software Foundation, 2008) and the R language for statistical computing (R Development Core Team, 2010) to automate the different sets of Monte-Carlo simulations. For each scenario tested, parameter space was comprehensively sampled with each parameter's distribution assumed uniform between the minimum and maximum bounds specified in Table 3.1. Thus, when testing each management scenario, we identically accounted for parameter uncertainty including the effects of interactions between input parameters. The Monte-Carlo simulations also allowed us to capture variability in environmental conditions from reef to reef (e.g. habitat, depth, exposure to urchin larvae). For each scenario tested, the total number of runs in each Monte-Carlo simulation is equal to 500 times the number of input parameters (Saltelli et al., 1999). The extended FAST also provided a robust model-independent ANOVA-like assessment of the relative contribution of input parameters to variance in model outputs (Saltelli et al., 1999), including those parameters associated with the different management levers (e.g. fishing mortality; see Table 4.1b and Fig. 4.5a and 4.7a).

4.3.3 Scenario testing (Table 4.1)

The sampling design across Monte-Carlo simulations was fixed to enable assessment of each scenario under identical conditions. The exceptions, of course, are those parameters related to the management levers themselves, namely lobster and sea urchin fishing mortality (F_{RL} and F_{CR}), lobster maximum legal size and lobster 'initial condition' (which defines the level of translocation of large lobsters to an area). Table 4.1 summarises the parameters specific to each of the separate management scenarios considered: culling sea urchins under a range of lobster fishing mortality, implementing a maximum legal size, or a combination of the previous two. We also tested the effects of culling or harvesting sea urchins under different lobster recruitment levels, given that lobster recruitment in the region may decrease with climate-driven changes in large-scale oceanographic features in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011). We investigated the effectiveness of these alternative management interventions (Table 4.1) in either (1) preventing overgrazing of macroalgae and formation of sea urchin barrens with simulations initiated in the seaweed-dominated state (Fig. 4.5 and 4.6), or (2) restoring dense, productive seaweed beds from sea urchin barrens with simulations initiated with the system supporting sea urchin barrens (Fig. 4.7 and 4.8). Fig. 4.9 is based on a subset of simulations that shifted either from the seaweed bed to sea urchin barrens (Fig. 4.9a), or back to dense seaweed cover (Fig. 4.9b). For each of these simulations, we recorded the time (in months) for the community to shift to the alternative state, then applied the kriging function from R's 'fields' package (R Development Core Team, 2010) to express the time for modelled community to shift as a function of the two most effective management levers (as determined from sensitivity analysis; see Fig. 4.5a and 4.7a), for rock lobster and sea urchin fishing mortalities. Finally, for comparison, we simulated lobster population dynamics with a simplified version of the stock assessment model (Eq. 4.1; see appendix A) that currently supports management of the Tasmanian southern rock lobster fishery in the central east coast of Tasmania (Punt and Kennedy, 1997). We assessed fishery performance (yield as annual catches) under a suite of different management scenarios, using both (1) the single species model that does not account for the risk of sea urchin barrens formation, and (2) TRITON (Fig. 4.10a and 4.10b).

4.4 Results

We consider results from simulations with TRITON along three main avenues: (1) identification of key thresholds in reef community dynamics; (2) comparison of the effectiveness of different management options to limit the effects of sea urchin destructive grazing of Tasmanian seaweed beds; and (3) performance of the lobster fishery under different management scenarios, comparing assessment approaches with and without consideration of the ecosystem effects of fishing.

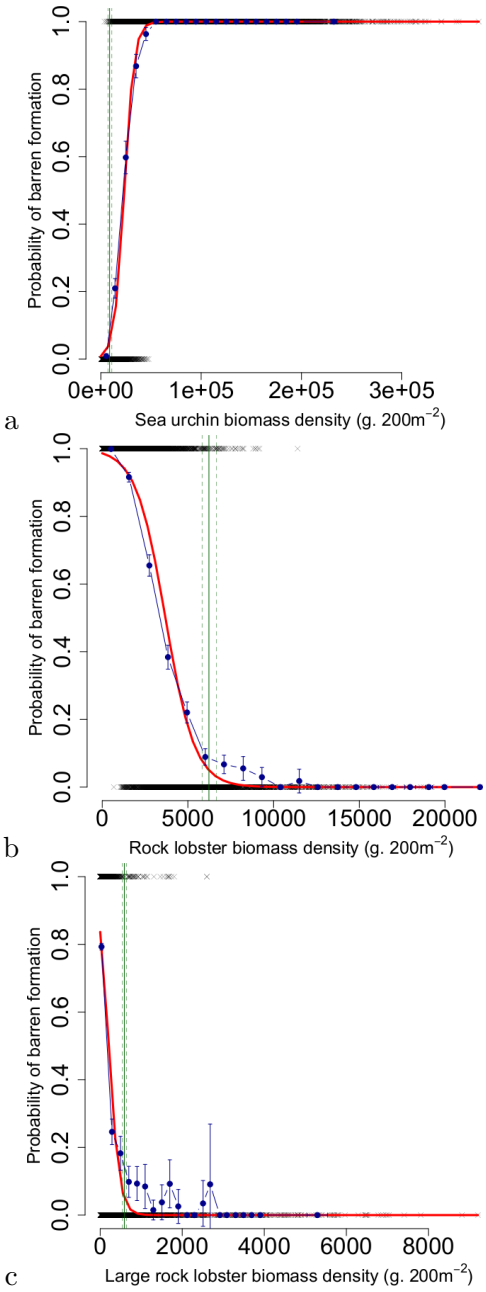


Figure 4.1: Probability of barren habitat forming (a, b, (c) through 8000 Monte-Carlo simulations initialised with high seaweed cover. Black crosses show the final state for each simulation. The blue line with dots and error bars (standard error) corresponds to all data points binned into 20 even intervals of biomass density (from 0 to the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled, i.e. (a) sea urchins; (b) rock lobster (all size classes combined); and (c) large lobsters (carapace length >140mm). Threshold points for the TRITON model to shift from the seaweed bed to the sea urchin barren state are marked by green solid lines with 95% confidence intervals given as dashed lines.

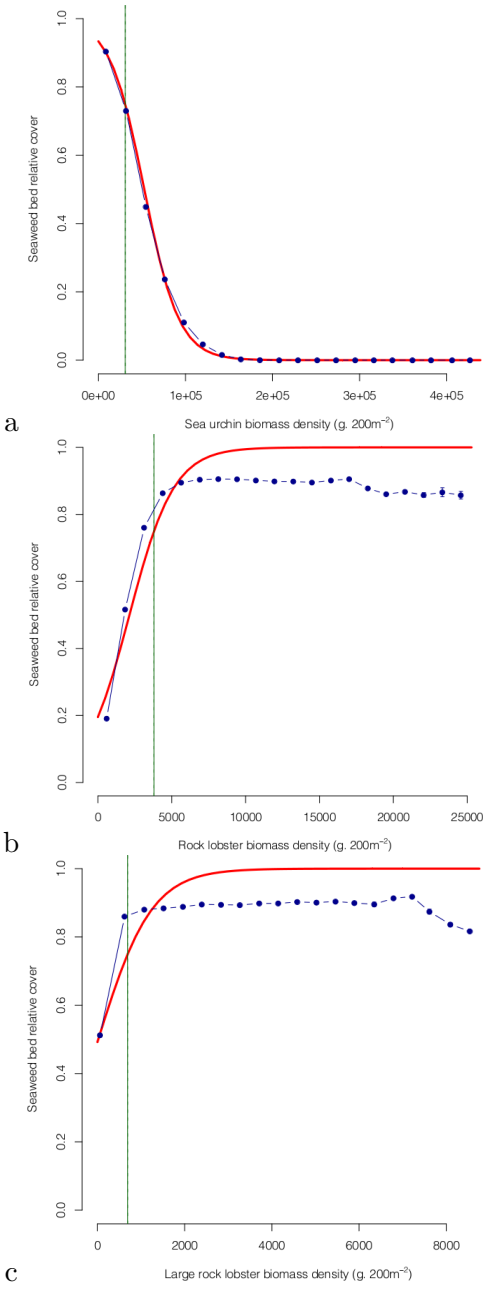


Figure 4.2: Proportion of seaweed bed cover through 8000 Monte-Carlo simulations initialised with high seaweed cover. The blue line with dots and error bars (standard error) corresponds to monthly model outputs binned into 20 even intervals of biomass density (from 0 to the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled, i.e. (a) sea urchins; (b) rock lobster (all size classes combined); and (c) large lobsters (carapace length >140mm). Threshold points for the TRITON model to shift from the seaweed bed to the sea urchin barren state are marked by green solid lines with 95% confidence intervals given as dashed lines.

Table 4.2: Summary statistics of binomial logistic models of the probability of a shift in community structure from the seaweed-dominated state to sea urchin barrens. The different models consider, either the probability of a community shift at the end of 50-year simulations (a, c, e), or the relative seaweed bed cover (b, d, f) as metrics to define threshold points in terms of biomass density of sea urchin (a, b), rock lobster (c, d) and large (carapace length superior to 140 mm) rock lobster (e, f).

a) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{CR}	-4.74	1.4 x 10^{-1}	-34.54	<2 x 10^{-16}
β_{CR}	2.03 x 10^{-4}	6.3 x 10^{-6}	32.15	<2 x 10^{-16}

Null deviance: 10233.9 on 7999 df; Residual deviance: 1879.9 on 7998 df

Variance explained: 81.6%; AIC: 1883.9; $B_{CRthreshold5\%}$ = 8858 (7099 - 10845) $g.200m^{-2}$

b) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{CR}	2.644	2.3 x 10^{-3}	1159	<2 x 10^{-16}
β_{CR}	-5.013 x 10^{-5}	5 x 10^{-8}	-1110	<2 x 10^{-16}

Null deviance: 4671322 on 4799999 df; Residual deviance: 1687397 on 4799998 df

Variance explained: 63.9%; AIC: 2798730; $B_{CRthreshold75\%}$ = 30832 (30689 - 30976) $g.200m^{-2}$

c) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL}	4.284	8.9 x 10^{-2}	47.9	<2 x 10^{-16}
β_{RL}	-1.16 x 10^{-3}	2.5 x 10^{-5}	-45.8	<2 x 10^{-16}

Null deviance: 10233.9 on 7999 df; Residual deviance: 4448.1 on 7998 df

Variance explained: 56.5%; AIC: 4452.1; $B_{RLthreshold5\%}$ = 6225 (5825 - 6660) $g.200m^{-2}$

d) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL}	-1.417	1.8 x 10^{-3}	-767	<2 x 10^{-16}
β_{RL}	6.627 x 10^{-4}	6.9 x 10^{-7}	962.2	<2 x 10^{-16}

Null deviance: 4671322 on 4799999 df; Residual deviance: 3052508 on 4799998 df

Variance explained: 34.6%; AIC: 4175824; $B_{RLthreshold75\%}$ = 3795 (3782 - 3808) $g.200m^{-2}$

e) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL140+}	1.63	3.5 x 10^{-2}	46.2	<2 x 10^{-16}
β_{RL140+}	-7.79 x 10^{-3}	2.6 x 10^{-4}	-29.26	<2 x 10^{-16}

Null deviance: 10233.9 on 7999 df; Residual deviance: 7207.2 on 7998 df

Variance explained: 29.6%; AIC: 7211.2; $B_{RL140+threshold5\%}$ = 588 (543 - 640) $g.200m^{-2}$

f) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL140+}	-3.1 x 10^{-2}	1.1 x 10^{-3}	-29.3	<2 x 10^{-16}
β_{RL140+}	1.626 x 10^{-3}	3.7 x 10^{-6}	439.8	<2 x 10^{-16}

Null deviance: 4671322 on 5099999 df; Residual deviance: 4236764 on 5099998 df

Variance explained: 9.3%; AIC: 5670606; $B_{RL140+threshold75\%}$ = 695 (690 - 699) $g.200m^{-2}$

4.4.1 Identifying key thresholds in reef community dynamics

Fig. 4.1, 4.2 and 4.3, 4.4 respectively focus on identifying key thresholds for the modelled reef community to shift forwards (from dense seaweed cover to sea urchin barrens) and 'backward' s (from barren habitat to recovered seaweed bed). Tipping points are characterised in terms of the probability of long-term barren formation (e.g. Fig. 4.1a) or, conversely, the probability of long-term restoration of the seaweed bed (e.g. Fig. 4.3a), as a function of the final biomass densities of sea urchins (e.g. Fig. 4.1a), lobsters (e.g. Fig. 4.2b), and large lobsters of carapace length >140 mm (e.g. Fig. 4.3c). Monitoring monthly seaweed cover through all Monte-Carlo simulations against biomass densities of the three groups (Fig. 4.2 and 4.1) provides an alternative view of tipping points in the dynamics. Red sigmoid curves in Fig. 4.1, 4.2, 4.3 and 4.4 represent binomial logistic models fitted against the biomass densities of (a) sea urchins; (b) all size classes of rock lobster; and (c) large lobsters (carapace length >140 mm). Summary statistics (i.e. parameter estimates, variance explained by the model, Akaike Information Criterion) for the GLM associated with the establishment of barren habitat (Table 4.2) or the recovery of seaweeds (Table 4.4) show that sea urchin biomass density is the most reliable predictor of the shift to urchin barrens (81.6% of the total variance explained by the GLM; Fig. 4.1a), while rock lobster biomass density best relates to the model's ability to return to a state of dense seaweed (62.7% of the total variance explained by the GLM; Fig.4.3b). The estimated thresholds clearly reveal the presence of a hysteresis in model dynamics, i.e. there are different tipping points associated with the 'forward' (Fig. 4.1 and 4.2; Table 4.2) and 'backward' (Fig. 4.3 and 4.4 ; Table 4.4) shifts. The community path and thresholds to restore the seaweed bed are different to the community trajectory of overgrazing driving seaweed beds to sea urchin barrens; sea urchin populations have to build to a biomass density of 10-40,000 g.200 m^{-2} for barren habitat to begin forming (Fig. 4.1a and 4.2a; Table 4.2a-b), while recovery of seaweeds on sea urchin barrens becomes highly likely only when there are virtually no sea urchins remaining on the reef (Fig. 4.3a and 4.4a; Table 4.4a-b). Note that, across all size classes combined, critical biomass densities of lobsters are of the same order, i.e. between 4000 and 6000 g.200 m^{-2}, for both the 'forward' (Fig. 4.1b and 4.2b; Table 4.2c-d) and the 'backward' shift (Fig. 4.3b and 4.4b; Table 4.4c-d). However, when considering the biomass density of large lobster (carapace length > 140 mm) only, the threshold biomass density for the seaweed bed to recover (Fig. 4.1c and

4.2c; Table 4.4e-f) is ∼3-4 times higher than the critical biomass density at which sea urchin barrens can start forming (Fig. 4.3c and 4.4c; Table 4.2e-f).

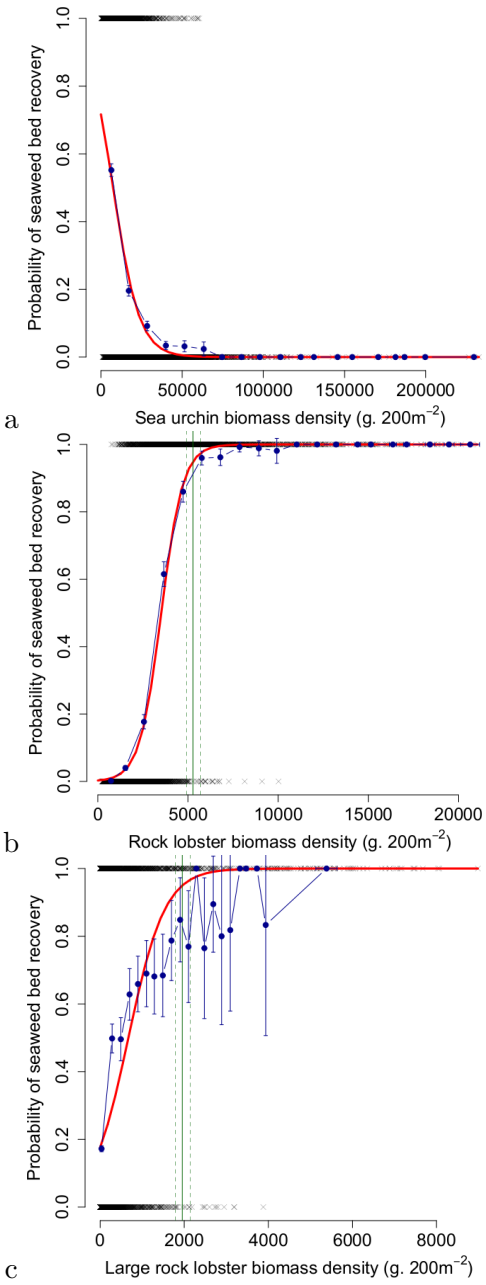


Figure 4.3: Probability of seaweed bed recovery through 8500 Monte-Carlo simulations initialised as sea urchin barrens (urchin culling as an extra parameter compared to 'forward' shift Monte-Carlo simulations). Black crosses show the final state for each simulation. The blue line with dots and standard error bars corresponds to data binned into 20 even intervals of biomass density (from 0 to the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled (a) sea urchins; (b) rock lobsters (all size classes combined); and (c) large lobster individuals (carapace length >140 mm). Threshold points at which the TRITON model shifts from sea urchin barren habitat back to the seaweed-dominated state are marked by green solid lines, with 95% confidence intervals shown as dashed lines.

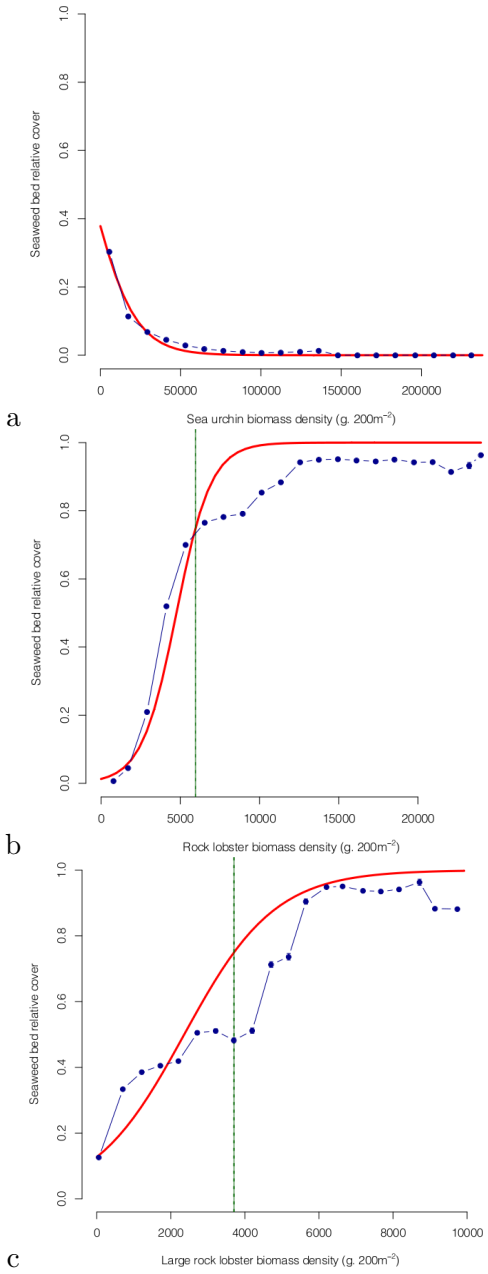


Figure 4.4: Proportion of seaweed bed cover through 8500 Monte-Carlo simulations initialised as sea urchin barrens (urchin culling as an extra parameter compared to 'forward' shift Monte-Carlo simulations). The blue line with dots and standard error bars corresponds to monthly model outputs binned into 20 even intervals of biomass density (from 0 to the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled (a) sea urchins; (b) rock lobsters (all size classes combined); and (c) large lobster individuals (carapace length >140 mm). Threshold points at which the TRITON model shifts from sea urchin barren habitat back to the seaweed-dominated state are marked by green solid lines, with 95% confidence intervals shown as dashed lines.

Table 4.4: Summary statistics of different binomial logistic models of the probability of a shift in community structure from sea urchin barren habitat to the seaweed-dominated state. The different models consider, either the probability of a community shift at the end of 50-year simulations (a, c, e), or the relative seaweed bed cover (b, d, f) as metrics to define threshold points in terms of the biomass density of sea urchin (a, b), rock lobster (c, d) and large (carapace length superior to 140 mm) rock lobster (e, f).

a) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{CR}	9.28 x 10^{-1}	5.2 x 10^{-2}	17.77	<2 x 10^{-16}
β_{CR}	-1.237 x 10^{-4}	3.5 x 10^{-6}	-35.15	<2 x 10^{-16}

Null deviance: 9670.1 on 8499 df; Residual deviance: 7316.6 on 8498 df

Variance explained: 24.3%; AIC: 7320.6; $B_{CRthreshold95\%}$ = -16295 (-16381 - -16295) $g.200m^{-2}$

b) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{CR}	-4.97 x 10^{-1}	1.9 x 10^{-3}	-259	<2 x 10^{-16}
β_{CR}	-7.34 x 10^{-5}	1.3 x 10^{-7}	-582	<2 x 10^{-16}

Null deviance: 4054306 on 5099999 df; Residual deviance: 3475451 on 5099998 df

Variance explained: 14.2%; AIC: 4082683; $B_{CRthreshold75\%}$ = -21747 (-21769 - -21725) $g.200m^{-2}$

c) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL}	-5.88	1.2 x 10^{-1}	-47.27	<2 x 10^{-16}
β_{RL}	1.67 x 10^{-3}	4 x 10^{-5}	42.12	<2 x 10^{-16}

Null deviance: 9670.1 on 8499 df; Residual deviance: 3604.9 on 8498 df

Variance explained: 62.7%; AIC: 3608.9; $B_{RLthreshold95\%}$ = 5277 (4903 - 5687) $g.200m^{-2}$

d) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL}	-4.349	3.4 x 10^{-3}	-1263.3	<2 x 10^{-16}
β_{RL}	9.134 x 10^{-4}	9.7 x 10^{-7}	943.6	<2 x 10^{-16}

Null deviance: 4054306 on 5099999 df; Residual deviance: 2252951 on 5099998 df

Variance explained: 44.4%; AIC: 2629804; $B_{RLthreshold75\%}$ = 5964 (5984 - 5944) $g.200m^{-2}$

e) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL140+}	-1.54	3.1 x 10^{-2}	-49.95	<2 x 10^{-16}
β_{RL140+}	2.30 x 10^{-3}	9 x 10^{-5}	25.15	<2 x 10^{-16}

Null deviance: 9670.1 on 8499 df; Residual deviance: 8307.0 on 8498 df

Variance explained: 14.0%; AIC: 8311; $B_{RL140+threshold95\%}$ = 1954 (1788 - 2147) $g.200m^{-2}$

f) **Parameter**	**Estimate**	**Standard error**	**z value**	**P value**
α_{RL140+}	-1.928	1.4 x 10^{-3}	-1386	<2 x 10^{-16}
β_{RL140+}	8.17 x 10^{-4}	1.7 x 10^{-6}	469	<2 x 10^{-16}

Null deviance: 4054306 on 5099999 df; Residual deviance: 3790144 on 5099998 df

Variance explained: 6.5%; AIC: 4389598; $B_{RL140+threshold75\%}$ = 3707 (3688 - 3725) $g.200m^{-2}$

4.4.2 Effectiveness of alternative management scenarios

Here we focus on the effects of alternative management interventions on the propensity to shift from either high seaweed cover to sea urchin barrens, or 'backward' to realise recovery of seaweed cover from sea urchin barrens. In addition to recruitment rates of lobsters being important in the overall dynamic, lobster fishing and direct sea urchin removal (by culling or harvesting) emerge as the main drivers of these shifts (Fig. 4.5a and 4.7a). Conversely, the initial state of the lobster population (high initial densities of lobster can represent initial translocations of lobsters from deeper waters) and the lobster maximum legal catch size only exert a marginal influence on the model's ability to shift. Under a range of lobster fishing mortality, we assessed different management interventions in terms of the probability of the model shifting forwards (Fig. 4.5b and 4.6a-d) or 'backward' s (Fig. 4.7b and 4.8a-d). The risk of sea urchin barrens forming increases markedly with lobster fishing mortality: from ∼15% with no fishing to ∼ 90% under intense harvesting of lobster ($F_{RL} > 2$ year^{-1}; Fig. 4.5b and 4.6a-d). Considering current fishing practise (black line; $F_{RL} \sim$ 1-1.5 year^{-1} and minimal legal catch size), direct removal of sea urchins (culling for harvesting) considerably mitigates the ecological effects of sea urchin destructive grazing, either to prevent barren formation (Fig. 4.5b) or restore sea urchin barrens to dense seaweed beds (Fig. 4.7b). Indeed, even a low intensity of sea urchin culling ($F_{CR} < 0.5$ year^{-1}) reduces the overall risk of barren formation by 15-20% and brings it to zero at low lobster fishing mortality (Fig. 4.6a). Conversely, implementing a maximum legal catch size significantly reduces the risk of seaweed destruction by 10-15% only if associated with a reduced fishing pressure ($F_{RL} < 0.8$ year^{-1}; Fig. 4.6c). Solely implementing a maximum legal size for lobster fishing, and taking no other action, does little if anything to facilitate recovery of seaweed beds (Fig. 4.8c). Additionally, the absolute value of the limit (between 135 - 165 mm of carapace length) of the maximum legal size has only marginal implications in the context of mitigating the effects of sea urchin destructive grazing of seaweed beds (Fig. 4.6b and 4.6b). Further, in combination with sea urchin culling, the implementation of a maximum legal size for lobster fishing still has only marginal effect in mitigating the effects of destructive grazing (Fig. 4.6c and 4.8c). It is only when and upper legal size is imposed along with significantly reduced catches, that risk of barren habitat formation reduces notably and the likelihood of recovery of seaweeds on barren habitat improves significantly. The caveat is that future uncertainty in lobster

recruitment in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011) can significantly limit the effectiveness of these management interventions (Fig. 4.8d and 4.8d) so that even when adopting the most efficient measures, i.e. combining sea urchin removal with a severe reduction in lobster fishing, destructive grazing may continue apace and seaweed recovery be unlikely if there is failure of lobster recruitment.

Fig. 4.9 only includes the proportion of the simulations that either did shift to sea urchin barrens (Fig. 4.9a) or where a dense seaweed bed was restored from the sea urchin barren state (Fig. 4.9b). While Fig. 4.5, 4.6, 4.7 and 4.8 describe the effects of management levers on the probability of shift in the modelled community, the patterns in Fig. 4.9 do not relate to probability of community shift. Fig. 4.9 only indicates mean transition times as extrapolated using R's *krig* function from these simulations that shifted. Thus, note that, regardless of the levels of sea urchin culling and rock lobster fishing, other factors such as recruitment rates or seaweed growth rate, can facilitate community shift and influence these mean transition times. The mean time for sea urchin barrens to establish in TRITON from an initial condition of dense seaweed cover is of the order of two decades, although time to barrens formation can decrease by a few years with increasing lobster fishing mortality (time to barrens decreases from ∼23 years at $F_{RL} = 0$ to ∼19 years at $F_{RL} = 2.5$ year^{-1}; Fig. 4.9a). Notably, the time to barrens formation is far more sensitive to the level of rock lobster fishing than rate of removal of sea urchins. Conversely, the time necessary for recovery and restoration of dense seaweed cover from sea urchin barrens declines with intensifying sea urchin removal. With heavy culling or harvesting of sea urchins ($F_{CR} = 2.5$), seaweed recovery can be effected in as little as 15 years (particularly is fishing pressure on lobsters is low), but extends to closer to three decades under no urchin culling and heavy fishing of lobster.

4.4.3 Lobster fishery performance under alternative management scenarios

Lobster catches dependent on fishing mortality estimated from simulations based only the single species stock assessment model are much higher than catch estimates from simulations using TRITON in which the potential for and consequences of sea urchin destructive grazing of seaweed beds are accounted for (Fig. 4.10a). As fishing intensifies, estimates based on the single species model asymptote, while catch estimates from TRITON are not only considerably lower than these from the single species model, they

begin to decline as fishing mortality (F_{RL}) rises above ~1.0 year^{-1}. This is because as sea urchin barrens start to form and the complex seaweed bed habitat is lost, the potential for juvenile lobsters to recruit gets reduced in TRITON. The optimal yield is displayed as a horizontal dashed line for each model and correspond to the 95% quantile of all simulated annual catches. Under current management practises (minimum legal catch size), the Ecologically Sustainable Yield (ESY) estimated with TRITON is reached at a lower fishing pressure ($F_{RL,ESY} \sim$ 0.4-0.5 year^{-1} associated with the green dashed line) than the Maximum Sustainable Yield (MSY) estimated from the stock assessment model ($F_{RL,MSY} \sim$ 0.7-0.9 year^{-1} associated with the red dotted line).

Comparison of long-term annual lobster catches dependent on fishing mortality under different options for management interventions indicated that the nature of the management approach will dramatically affect catch. These results are derived from simulations with TRITON in which the community was initialised in the seaweed bed state. Out of all management options and across the whole range of potential fishing pressure on lobster, direct removal of sea urchins (green line) delivers the highest catches. Implementing a maximum legal size (set between 135-165 mm of carapace length) (red line) enhances fishery productivity at moderate to high fishing mortality but does not significantly affect fishery productivity at low fishing pressure ($F_{RL} <$ 0.4 year^{-1}) relative to current practises (black line) based on a minimum legal size and $F_{RL} \sim$ 1-1.5 year^{-1}. Overall, any management intervention implemented in addition to current regulations act to improve fishery productivity by enhancing predation control on sea urchins and minimise the impacts of sea urchin destructive grazing on reef productivity.

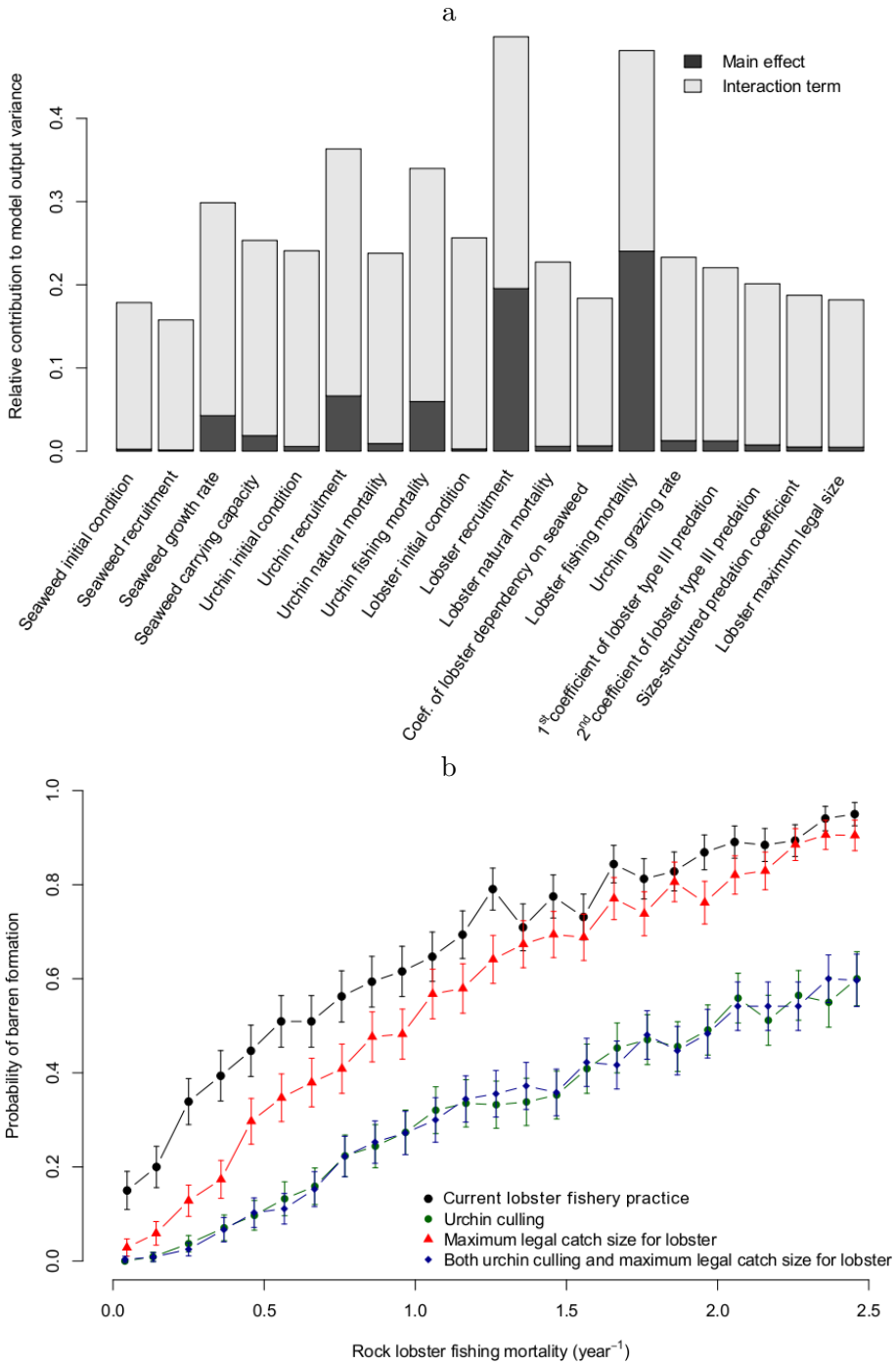


Figure 4.5: Effects of alternative management measures on the long-term risk of barrens formation in the model: (a) Extended FAST sensitivity indices showing the relative influence of all inputs on model behaviour (based on the first axis of the PCA conducted on normalised mean biomass densities for the last 10 years of simulations). Risk of barren formation against lobster fishing mortality (b) under different general management interventions (direct removal of sea urchin or imposing a maximum legal size for lobsters, or both). Error bars correspond to the standard error across Monte-Carlo simulations.

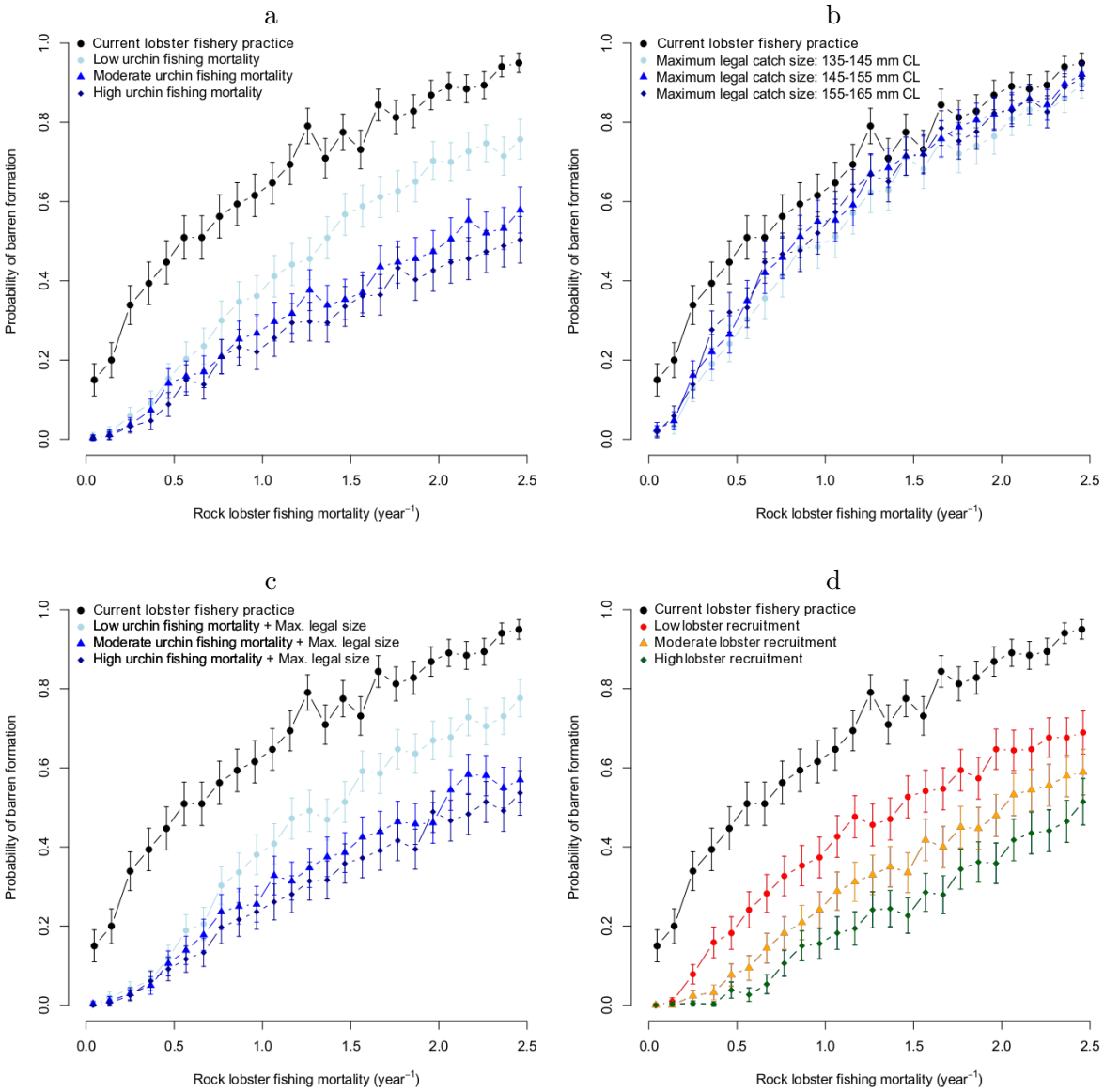


Figure 4.6: Risk of barren formation against lobster fishing mortality under different management interventions (direct removal of sea urchin or imposing a maximum legal size for lobsters, or both): (a) with different levels of sea urchin culling, (b) with different maximum legal catch sizes for lobster, (c) with a combination of maximum catch size for lobster and different sea urchin culling mortalities, and (d) with sea urchin culling under different levels of lobster recruitment. All Monte-Carlo simulations are initiated in the seaweed bed state. Error bars correspond to the standard error across Monte-Carlo simulations.

4.5 Discussion

4.5.1 Thresholds in Tasmanian rocky reef dynamics

Management of marine ecosystems is increasingly moving towards a threshold approach to diminish the risk of phase shifts to some less desirable alternative community state (Mumby et al., 2007; Suding and Hobbs, 2009; Briske et al., 2010; Osman et al., 2010; McClanahan et al., 2011; Melbourne-Thomas et al., 2011*b*). System-specific ecosystem models provide unique tools to explore these thresholds in community dynamics (Scheffer and Carpenter, 2003; de Young et al., 2008). Among other marine examples, several applications have successfully described thresholds in coral reef dynamics (e.g. Mumby et al., 2007; Fung et al., 2011; McClanahan et al., 2011). In this paper, modelling the dynamics of a temperate reef community informs important reference points related either to the risk of a shift from high seaweed cover to sea urchin barrens (Fig. 4.1 and 4.2; Table 4.2), or alternatively to the probability for seaweeds to recover on fully established barren habitat (Fig. 4.3 and 4.4; Table 4.4). The differences in threshold biomass densities of sea urchins, rock lobsters (total), and large rock lobsters (carapace length >140 mm) between the 'forward' shift (from seaweed bed to sea urchin barren habitat) and the 'backward' shift (recovery of seaweed cover) reflect the presence of a hysteresis in community dynamics as suggested by field observations (Ling et al., 2009*a*). Importantly, model dynamics indicate that avoiding the critical tipping point beyond which extensive sea urchin barrens establish is achievable under sound management (Fig. 4.1 and 4.2). However, the restoration of seaweed beds once sea urchin barrens have formed constitutes a major challenge (Ling et al., 2009*a*) that requires depletion of the sea urchin population to very low levels (virtually back to zero) (Fig. 4.3 and 4.4). Note also that, even though critical biomass densities of lobster for both shifts are of the same order (4000-6000 g.200 m^{-2}), reaching this threshold density of lobster will be more challenging on poorly productive sea urchin barren habitat than in dense seaweed beds (Johnson, unpublished data; Johnson et al., 2005; Ling, 2008).

When considering estimates of thresholds in rocky reef community dynamics, let us keep in mind that the precision and the accuracy of absolute predictions from complex ecological models depend on the reliability of all input parameters. In this context, simulation outcomes are often interpreted in relative terms (e.g. comparisons among alternative

scenarios; Smith et al., 2011) rather than as absolute predictions (Francis and Shotton, 1997). However, absolute estimates of thresholds in community dynamics are essential to a sound management of Tasmanian rocky reef community, and if managers do not have access to the best absolute estimates that researchers can provide, even with all their caveats, they will make management decisions anyway. The simulations with TRITON, based upon the best available information about Tasmanian reef ecology, currently provide the most reliable and conservative estimates of thresholds in reef community dynamics.

Binomial logistic GLMs relate the probability of community shifts to the biomass density of the different model groups. Goodness-of-fit criteria can be assessed in terms of the amount of variance in model behaviour explained, and help to identify the model groups that best relate to changes in community state, as defined in terms of the presence or absence of a dense macroalgal canopy. For example, of the three groups considered (i.e. sea urchins, rock lobsters and large rock lobster), sea urchin biomass density is the best predictor of the 'forward' shift (with 63.9 - 81.6% of the total variance captured by the GLMs), while the 'backward' shift most closely relates to rock lobster standing density (with 44.4 - 62.7% of the total variance captured by the GLMs). The GLM fits provide a robust tool to determine threshold points for management depending on acceptable risk levels. Here, we considered tipping points associated with a 5% probability of barrens formation, a 95% chance of seaweed bed restoration, or 75% of seaweed cover (above which sea urchin destructive grazing has marginal effects on macroalgal cover). Note that these arbitrary thresholds are more conservative than the inflection point of the fitted logistic GLM (associated with 50% of seaweed cover), where the slope is maximal and where small changes in standing biomass densities can induce large shifts in community structure (van Nes and Scheffer, 2004). It is important to recognise that the thresholds used in the fitted binomial models can easily be revised depending on the level of risk averseness that management and/or industry wish to adopt. Thus, logistic binomial models provide a convenient and objective approach to describe the risk of ecosystem shift as a function of the densities of the different model groups. However, changing these risk levels within reasonable bounds is unlikely to have any effect on the qualitative results and associated conclusions.

In field experiments, large lobsters (carapace length >140 mm) physically able to prey on all size classes of emergent *C. rodgersii*, were identified as the only efficient predator

on emergent sea urchins on Tasmanian east coast reefs and thus as key ecosystem players to control sea urchin populations and limit the risk of destructive grazing (Ling et al., 2009*a*). In TRITON, all medium to large sizes of lobster (carapace length = 115-140 mm) contribute to predation control on the sea urchin population (Fig. 4.1b, 4.2b, 4.3b, 4.4b; Tables 4.2c-d and 4.4c-d) and the biomass density of large rock lobsters alone does not provide the best predictor of phase shift (Fig. 4.1c, 4.2c, 4.3c, 4.4c; Tables 4.2e-f and 4.4e-f). This apparent discrepancy between field experiments and model simulations reflects that in TRITON we allow intermediate sizes of lobsters (carapace length = 115-140 mm) to prey on smaller sizes of emergent sea urchins (test diameter = 70 - 90 mm) as observed in tank experiment (Ling et al., 2009*a*). Therefore, intermediate sizes of lobster contribute to controlling the whole urchin population and can prevent emergent urchins reaching adult size in the model. However, this behaviour in TRITON does not necessarily occur in reality, where habitat complexity can reduce predatory interactions between lobsters and sea urchins (Ling et al., 2009*a*). Thus, predatory interactions between smaller size classes of lobsters (110-140 mm of carapace length) and sea urchins are potentially over-represented in the model. Alternatively, the discontinuous recovery of seaweed cover from the barren state as the biomass density of large lobster increases (Fig. 4.4c) may also relate to the hysteresis in model dynamics, with three more or less distinct phases of recovery from the barren state: 1) the first phase of recovery (biomass density of large lobster $<$ 4000 g. 200 m^2) corresponds to initial rebuilding of the seaweed bed (mean seaweed cover $<$ 50%) as grazing pressure is progressively reduced and macroalgal recruitment and regrowth resume on urchin barrens. On this part of the graph, sea urchin grazing mitigates complete regrowth of the seaweed bed and only a marginal proportion of simulations shift back to a dense seaweed state; 2) Then, in the second phase of the graph (biomass density of large lobster $>$ 4000 g. 200 m^2), mean seaweed cover gets greater than 50% as urchin population numbers are further depleted, with a dominant proportion of simulations indicate a shift back to full seaweed cover. Note that seaweed logistic growth reaches a maximum at 50% cover (the inflection point of the logistic model), so once the seaweed bed recovers to 50% cover, seaweed growth rate is the most likely to overwhelm any effects of grazing by the remaining sea urchins); 3) Once the biomass density of large lobster exceeds 6000 g. 200 m^2, recovery of dense seaweed bed cover is almost certain (sea urchins are then present at marginal densities with such high densities of predation-capable lobster).

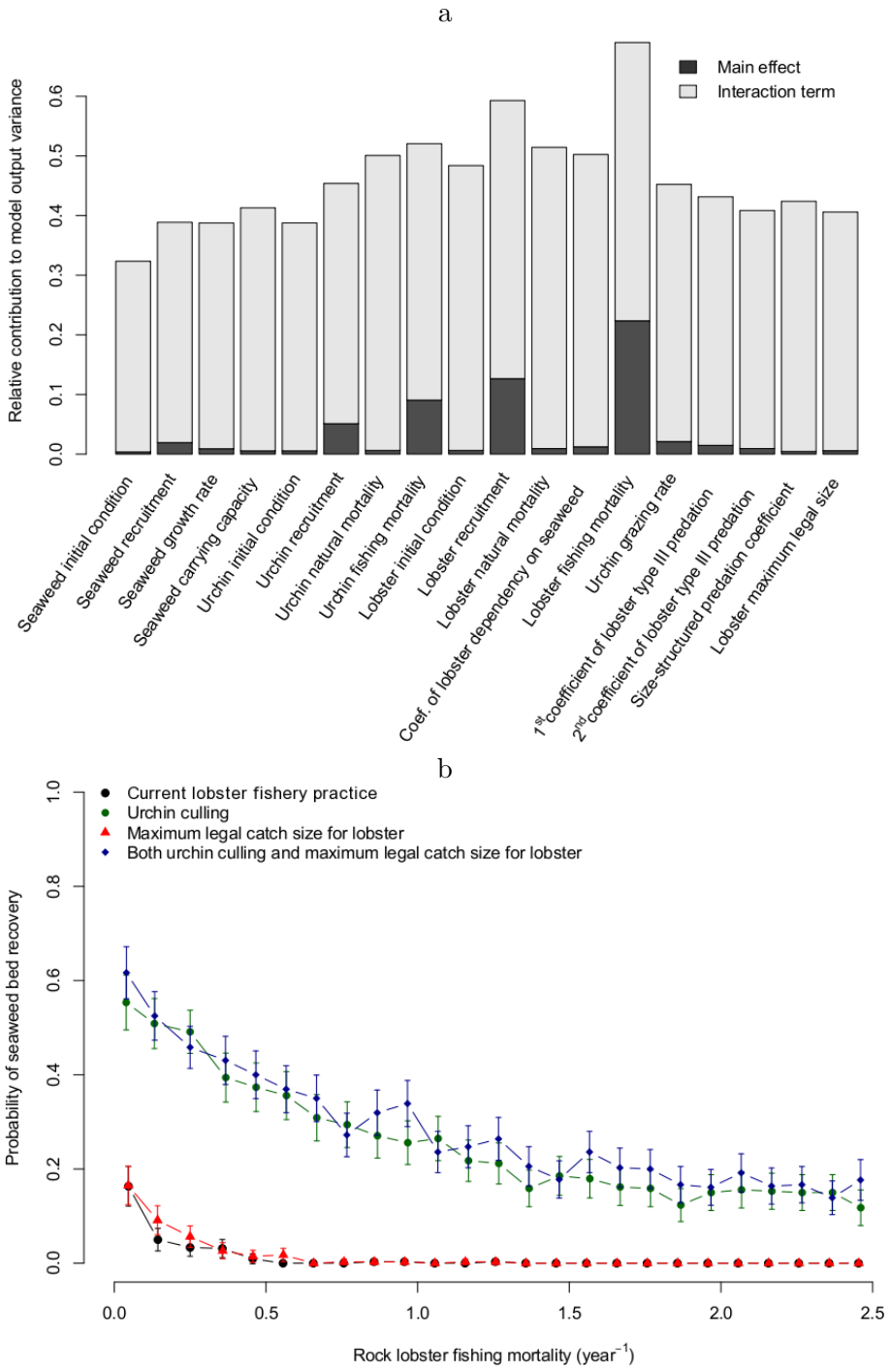


Figure 4.7: Effects of alternative management measures on the long-term probability of recovery of seaweeds on sea urchin barrens. (a) Extended FAST sensitivity indices showing the relative influence of all inputs on model behaviour (based on first axis of the PCA on normalised mean biomass densities for the last 10 years of simulations). Probability of seaweed bed recovery against lobster fishing mortality (b) under different general management interventions (direct removal of sea urchins, or imposing a maximum legal size for lobsters, or both). Error bars correspond to the standard error across Monte-Carlo simulations.

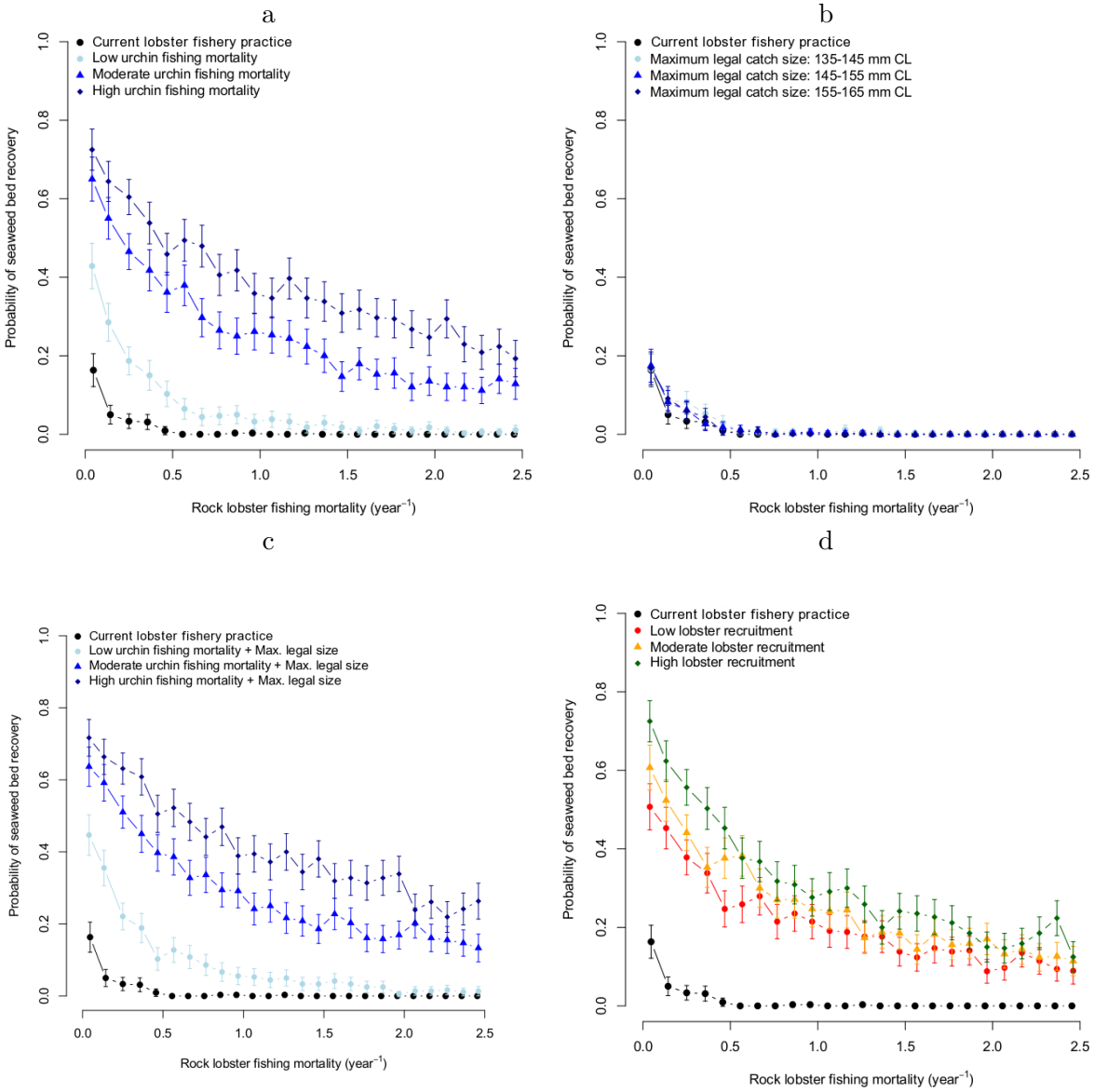


Figure 4.8: Probability of seaweed bed recovery against lobster fishing mortality under different specific management interventions (direct removal of sea urchins, or imposing a maximum legal size for lobsters, or both): (a) with different levels of sea urchin culling, (b) with different maximum legal catch sizes for lobster, (c) with a combination of establishing a maximum catch size for lobster (carapace length = 135-165 mm) and direct culling of sea urchins, and (d) with sea urchin culling under different levels of lobster recruitment. All Monte-Carlo simulations are initiated in the sea urchin barren state. Error bars correspond to the standard error across Monte-Carlo simulations.

4.5.2 Alternative management options against sea urchin destructive grazing of seaweed beds

Of all the parameters related to management intervention, fishing of rock lobster and sea urchins demonstrate the highest influence on the model's ability to demonstrate 'forward' (Fig. 4.5a) or 'backward' (Fig. 4.7a) phase shifts. In addition to current management practises for the lobster fishery (i.e. regional quotas and minimum legal size), culling of sea urchins constitutes the most effective management response to minimise effects of destructive grazing in TRITON, and this is particularly effective when combined with a marked reduction in lobster fishing. We acknowledge however that in reality extensive culling or harvesting of sea urchins is unlikely to occur at a sufficient scale to be effective in mitigating risk of barrens formation at a whole-of-coast scale. Despite repeated examples of large scale depletion, and sometimes collapse, of sea urchin populations elsewhere in the world through overfishing (Andrew et al., 2002), *C. rodgersii* does not have high market value given features of its taste, colour, texture and preservability, and so at this stage opportunity to develop a large fishery on the sea urchin is limited. Moreover, the greatest extent of *C. rodgersii* barrens is in waters 15-30 m depth (Johnson et al., 2011), which greatly limits accessibility of divers to the resource.

On their own, interventions to rebuild rock lobster populations as natural predators of sea urchins (e.g. by imposing a maximum legal catch size, and reducing lobster fishing) only marginally reduce the risk of sea urchin barren formation (from ∼60% to ∼50%), and have no effect in improving the likelihood of restoring dense productive seaweed beds (which is effectively 0%), unless lobster fishing is reduced considerably from current levels. Implementation of a maximum legal catch size, currently a focus of discussion between managers and the Tasmanian rock lobster fishing industry, can only effectively mitigate the effects of sea urchin destructive grazing if associated with low to moderate lobster fishing mortality. Specifically, implementing a maximum catch size can reduce the probability of barren formation by 10-20%, but only when F_{RL} is less than 0.7 year^{-1} (Fig. 4.5 and 4.6). The effects of implementing a maximum legal catch size may arise in part because size-structured predation in TRITON allows for interactions between medium sizes of lobsters and small emergent urchins. Thus, sea urchin population control through predation in the model relies on the whole spectrum of medium (110-140 mm of carapace length) to large (carapace length >140 mm) size classes of lobster rather than solely on large

lobsters predating emergent sea urchins (Ling et al., 2009*a*). Thus, while empirical data indicate clearly that only large lobsters (carapace length>140 mm) are able to predate emergent sea urchins (70-130+ mm test diameter; Ling et al., 2009*a*), in developing the model we assumed that medium sized lobsters have access to medium sized (<70 mm test diameter) sea urchins, which are largely cryptic within the interstices of the reef matrix (while this assumption is in need of empirical validation, it is an exceedingly difficult task). Additionally, TRITON's low sensitivity to initial abundances of lobster (Fig. 4.5a or 4.7a) suggests that single events translocating large lobsters (usually fished in deep water) onto shallow exposed reefs have virtually no influence on the long-term mitigation of sea urchin destructive grazing of seaweed beds. Note, however, that regular artificial enhancement of lobster populations through translocation (see Gardner and Van Putten, 2008), captured in Fig. 4.5d and 4.7d as high lobster recruitment scenarios, can considerably improve management interventions against sea urchin destructive grazing.

All our results depict the presence of a hysteresis in community dynamics, which has strong implications for management. Preventing the further establishment of sea urchin barrens in eastern Tasmania arguably remains a realistic possibility (Fig. 4.5 and 4.6), however once extensive barren habitat has formed, restoration efforts palatable to the lobster fishing industry are likely to be highly ineffective at facilitating recovery of seaweed cover (Fig. 4.7 and 4.8). In particular, even total cessation of lobster fishing on barren habitat (Fig. 4.7b) is unlikely to facilitate the recovery of seaweeds due to the low productivity of the barren habitat (Johnson et al., 2005; Ling, 2008). Note also that, when a shift occurs, transition time from one state to the other takes from two to three decades (Fig. 4.9). However, lobster fishing diminishes the duration of the 'forward' shift and increases the time for seaweed bed recovery, while sea urchin culling has the opposite effect. Under controlled experimental conditions where all grazers are totally excluded from small barren patches, full recovery of dense seaweed beds takes about two years (Ling, 2008). The recovery in two years applies only to the early stages in the formation of incipient barrens. In similar circumstances, the recovery of the seaweed bed in the absence of grazers also takes two years in TRITON (cf. Appendix A and the definition of the logistic growth model for the seaweed bed). However, under persistent sea urchin recruitment and sufficient habitat complexity (e.g. shelter crevices), permanent eradication of sea urchins on barren grounds is unachievable at wider scales over a few years (Johnson et al., unpublished data). In marked contrast with the prompt recovery on incipient barren, even when

grazers are depleted to quite low densities, the simulations suggest that the recovery of the seaweed beds on extensive barrens typically takes over two to three decades when relying on a combination of direct urchin culling and natural control through lobster predation. Thus, while preventing the establishment of sea urchin barrens in the first place can be accommodated practicably under current management schemes, implementing 30+-year management plans to restore seaweed beds is less realistic.

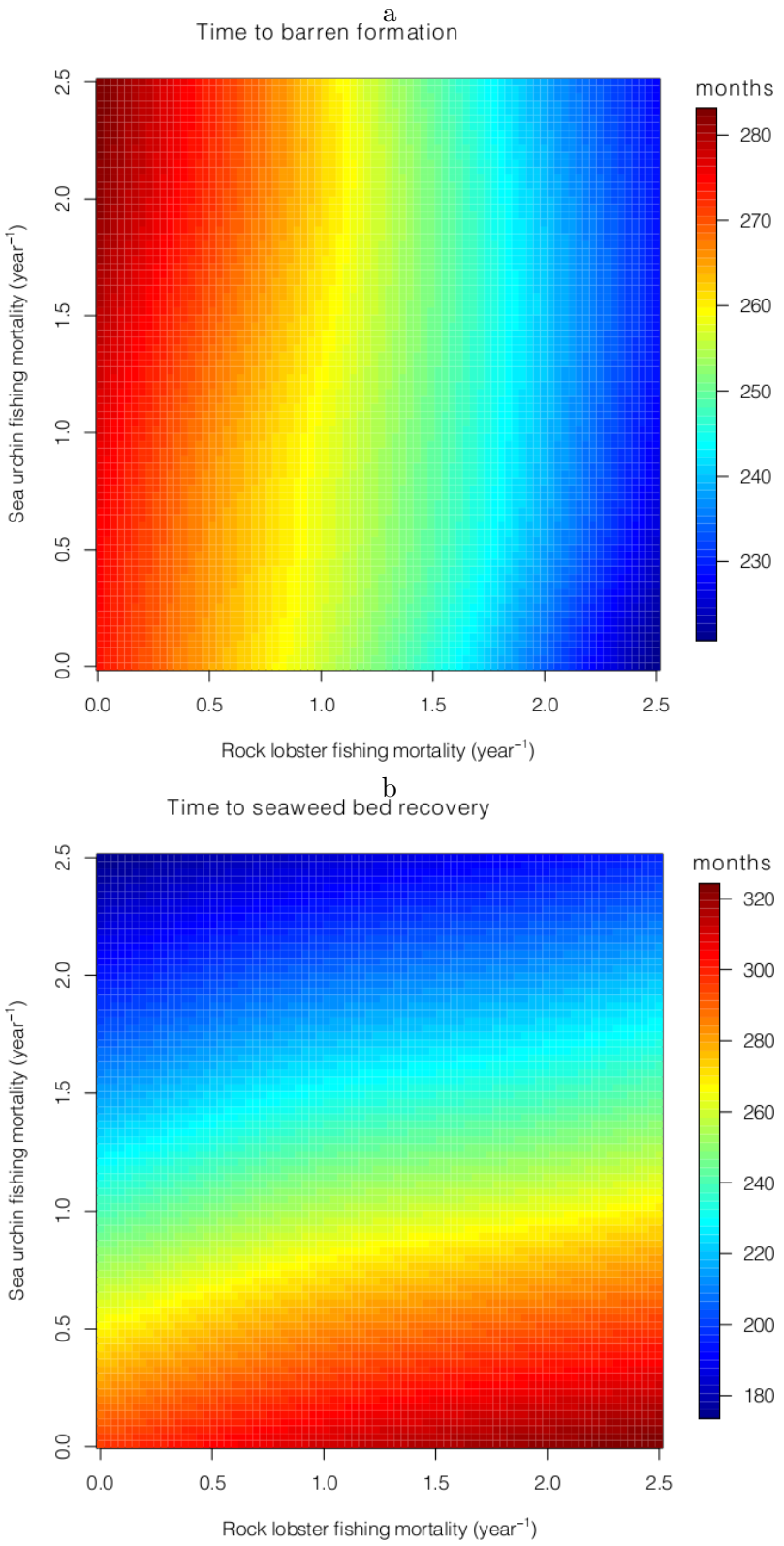


Figure 4.9: Time (months) for the modelled community to shift (a) 'forward' from dense seaweed cover to sea urchin barrens, or (b) 'backward' from sea urchin barrens to recovery of dense seaweeds as a function of rock lobster and sea urchin fishing mortalities. The surface plot was produced from final results from 8500 Monte-Carlo simulations using the *krig* function from Rs *field* package.

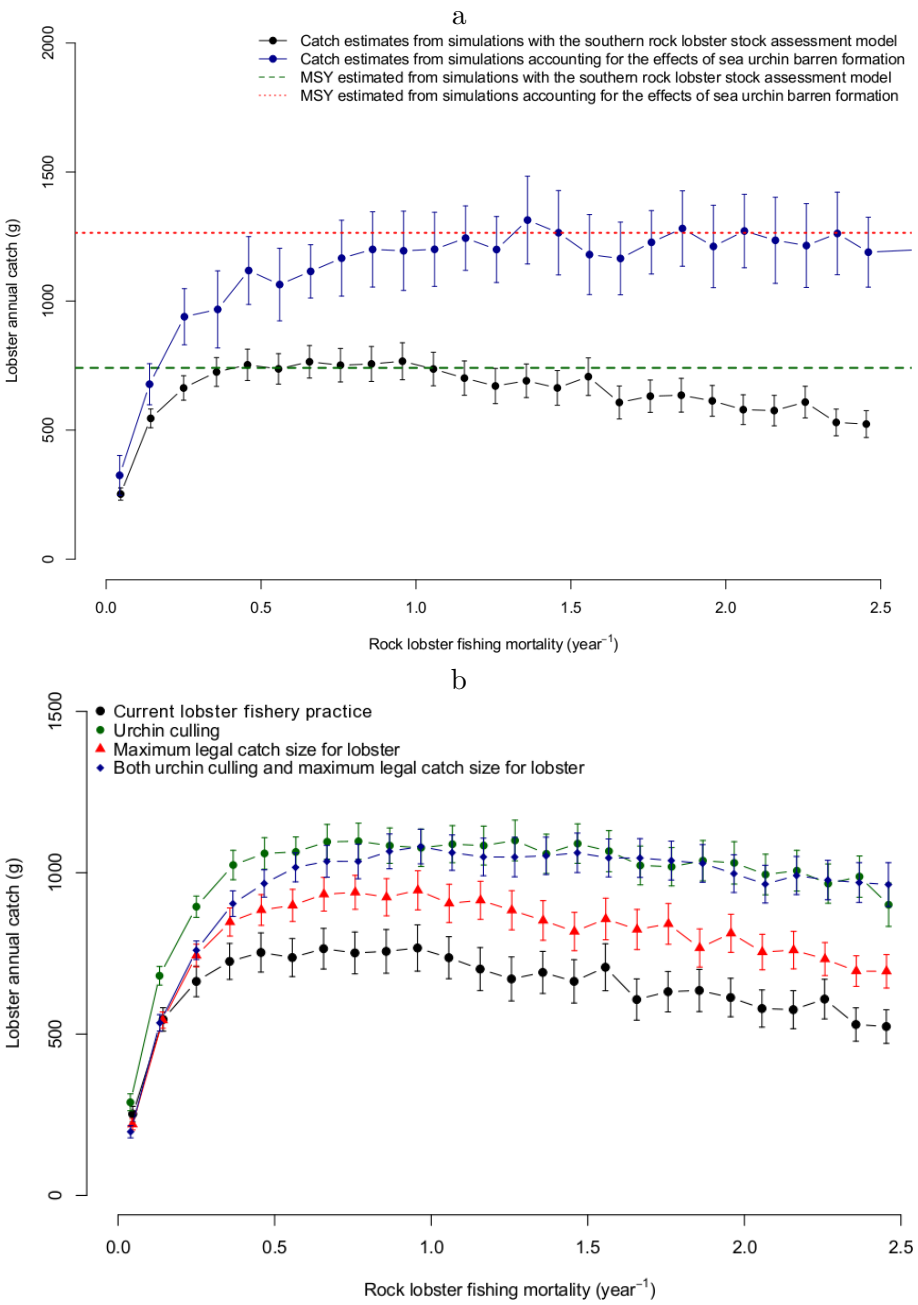


Figure 4.10: (a) Yield curves or annual equilibrium catches (g per 200 m^2 patch of reef) of rock lobster from simulations with a single species lobster population model (blue) and with the TRITON model (black) that accounts for the risk and consequences of sea urchin barren formation and the consequences of this shift in community and habitat structure for lobster productivity. The red and green dashed lines show optimal yields estimated from Monte-Carlo simulations based on the single species (Maximum Sutainable Yield) and the TRITON model (Ecologically Sustainable Yield) respectively. (b) Annual lobster catches estimated using TRITON under alternative management interventions (either removal of sea urchins, or imposing a maximum legal size for lobsters (carapace length = 135-165 mm) or both). Current fishery practice is shown by the black line. Error bars correspond to the standard error across Monte-Carlo simulations.

While model simulations provide valuable information about the effectiveness of different management levers to mitigate sea urchin destructive grazing, we keep in mind that TRITON is a model, i.e. a simplified representation of reality. The responses of real Tasmanian rocky reef communities to management intervention may prove more complex and variable than the mean patterns observed through simulations. An important result is that the modelled community is nearly as sensitive to mean recruitment rates of both lobsters and sea urchins, and to the intrinsic growth rate of the seaweed assemblage, as to practical management levers as associated with lobster fishing mortality or sea urchin culling mortality (Fig. 4.5a and 4.7a). Thus, it is possible that environmental factors can significantly counter the impact of management intervention, e.g. different scenarios in terms of future levels of regional lobster recruitment (see Johnson et al., 2011) can considerably influence the outcome of management intervention. Spatial variability in lobster and sea urchin recruitment rates, and in seaweed growth rates, often reflects heterogeneity of habitat (e.g. suitable substratum for recruiting larvae, exposure to storms, depth and light exposure, nutrient levels to drive primary production). While our results through Monte-Carlo simulations capture the mean dynamics across the spatial variability of Tasmanian reef communities, patchy heterogenous reef habitat will display a gradient of responses to particular management interventions.

While this study addresses the effectiveness of alternative management interventions, it is beyond the scope of the work to fully assess the practical considerations related to their implementation. Nonetheless, a brief analysis of the management environment is appropriate. In recent years, lobster fishing mortality in eastern Tasmania has varied around 1-1.4 year^{-1} over the last few years (K. Hartmann, unpublished data). While a moderate reduction in lobster fishing pressure is possible for the east coast of Tasmania (down to $\sim$ 0.8 year^{-1}), a sharp decrease (below 0.5 year^{-1}) is highly unlikely in the current management environment. We have already raised practical considerations related to direct harvesting of sea urchins. Even if the focus of culling is only at a local scale, for example in targeting patches particularly productive for abalone, we have shown that abalone divers engaged in culling sea urchins while they are fishing for abalone has limited effectiveness (Johnson, unpublished data). Moreover, effective culling of sea urchins by divers is particularly challenging given the complexity of reef habitat, nocturnal activity of the sea urchins, the depth limitation of diving operations, and the cryptic nature of small and medium-sized individuals. A small-scale fishing and processing industry for

C. rodgersii was recently launched in St. Helens in the northeast of Tasmania, but the possible extent and intensity of harvesting is yet to be assessed. For practical reasons, commercial harvesting by divers is restricted to shallow reefs (depth < 25 m). Note also that developing a commercial dive-based fishery for *C. rodgersii* is likely to favour sustainable harvesting of urchin rather than restoration of dense seaweed beds. The implementation of a maximum legal catch size for lobsters has been considered seriously by both managers and the fishing industry for the regions where *C. rodgersii* occurs. The underlying logic is to afford protection to lobsters large enough to be capable of predating emergent *C. rodgersii*. However, results from the simulation model indicate that this measure can only usefully mitigate barren formation in combination with a reduction in lobster fishing to below F=0.8 year^{-1}. The simulations indicated that simultaneous implementation of a combination of these measures is most likely to mitigate sea urchin barren formation at a local scale. Reducing fishing mortality is fundamental, and will see greatest effect when conducted in conjunction with targeted culling and, to a lesser extent, imposition of an upper size limit in the lobster fishery. Further assessment of the practicability and cost-effectiveness of each potential management lever in a formal cost-benefit analysis would be a useful next-step to complement the ecological assessment presented here.

4.5.3 Ecosystem-based fishery management and the importance of accounting for the ecological role of target species

The Tasmanian southern rock lobster fishery serves as a useful example to emphasise both 1) the importance of accounting for the broader ecological role of commercially fished species when defining reference points for fishery management, and 2) the value of implementing management measures to optimise long-term performance and sustainability of the fishery (Fig. 4.10).

Our analyses provide a powerful argument for management of the Tasmanian rock lobster fishery to move away from decisions based on single species assessment, towards ecosystem-based reference points; more formally, to transition from a focus on maximum sustainable yield (MSY) towards an ecologically sustainable yield (ESY) (Mace, 2001; Zabel et al., 2003; Hall and Mainprize, 2004; Walters et al., 2005). Our analysis indicates that large rock lobster individuals contribute an important ecological service in maintaining functioning

of dense productive seaweed beds by controlling sea urchins responsible for destructive grazing (Ling et al., 2009*a*), and that $F_{RL,MSY}$, the fishing mortality associated with the maximum sustainable yield estimated using the single species Tasmanian rock lobster fishery assessment model, corresponds to a level of fishing pressure that constitutes ecosystem-based overfishing (Murawski, 2000; Mace, 2001). Indeed, the single-species approach does not account for the depensation effect in lobster population dynamics, i.e. the decrease in juvenile recruitment due to increased risk of habitat loss at low density of legal size lobsters. Under current management practise, $F_{RL,MSY}$ should be seen as a limit with high associated risk, rather than an ecologically desirable target point for reef communities. The reference point for optimal sustained fishery performance, or fishing mortality associated with the ecologically sustainable yield ($F_{RL,ESY}$), needs to account for the ecosystem services delivered by rock lobster to rocky reef communities, and this level is notably more conservative than the $F_{RL,MSY}$ coming out of the single species population model (Hall and Mainprize, 2004). As a direct consequence of barren habitat affecting lobster recruitment potential, simulations with TRITON provide estimates of fishery productivity that are almost twofold lower than those from the single species model. The barren habitat is well recognised as an undesirable reef state with reduced productivity for both abalone and lobster fisheries in eastern Tasmania (Johnson, unpublished data; Johnson et al., 2005; Ling, 2008), but we acknowledge that the actual magnitude of this loss of fishery productivity is coarsely represented (unpublished data, CR Johnson or Ling et al., in preparation) in TRITON and requires cautious interpretation.

In the context of Tasmanian reef communities exposed to the invasive *C. rodgersii*, any management intervention implemented specifically to mitigate sea urchin destructive grazing of seaweed habitat additional to current regulations (which are based on transferable quota, a defined fishing season, and a minimum legal catch size) is likely to improve fishery productivity, even if only marginally (as is the case, for example, when implementing a maximum legal size). Additional management interventions against destructive grazing of seaweed beds, such as direct culling of sea urchins, can modify the lobster fishery yield curve and displace the ecologically sustainable yield towards higher lobster fishing mortality relative to status quo. For example, culling of sea urchins together with a moderate reduction in lobster fishing ($F_{RL} \sim$ 0.7-0.8 year^{-1}) can deliver both better performance in the lobster fishery (Fig. 4.10b) while reducing the risk of barrens formation to $\sim 30\%$ (Fig. 4.6a). We add the caveat that representing fishing as a simple

instantaneous mortality term does not fully capture the complex interactions between the fishery and the target species (e.g. catchability). To this extent both lobster fishing and urchin culling are expressed rather theoretically in TRITON and the model does not realistically capture current quota management defined in terms of Total Allowable Catch. Overall, we however contend that the different sets of Monte-Carlo simulations reveal the effectiveness of alternative management interventions on both long-term ecological state of rocky reef communities and productivity of the lobster fishery.

4.6 Conclusions

Using Monte-Carlo simulations with a model that captures the potential for alternative community states in lobster-sea urchin-seaweed dynamics, we provide estimates of key thresholds in Tasmanian rocky reef communities. These tipping points, which define important reference points to mitigate the effects of sea urchin destructive grazing through predation control, indicate the presence of a hysteresis in community dynamics that is also reflected in the model. For management, the hysteresis emphasises the need to focus on preventing the formation of sea urchin barrens rather than on the far more challenging task of restoring seaweed beds after extensive barren habitats has established. Where it can be practically implemented, direct culling or harvesting of sea urchins together with a reduction in lobster fishing is the most ecologically effective intervention to minimise the impact of the sea urchin grazing on Tasmanian reefs. This approach is likely to be more effective in both the short and longer term than intervention aimed exclusively at building the lobster population (e.g. by only reducing lobster fishing or implementing a maximum legal catch size). Our model simulations highlight the need for management of the Tasmanian lobster fishery to better account for the pivotal ecological role of lobsters in this system, and to revise key target points accordingly, and provide a valuable assessment of some of the tradeoffs in terms of both long-term ecological outcomes and fishery productivity associated with alternative management interventions. The important next step in this process is to implement a detailed cost-benefit analysis across the various management alternatives we have identified.

Chapter 5

Synthesis: Models to assist ecosystem-based management of rocky reef communities and the rock lobster fishery in eastern Tasmania

This thesis presents a suite of 'minimum-realistic' models (sensu Fulton et al., 2003*a*) developed to inform an ecosystem-based approach to management of rocky reef communities and the associated rock lobster fishery in eastern Tasmania. The modelling approaches build on available information about Tasmanian reef ecology (e.g. empirical observations, field experiments or existing models) to provide improved understanding and prediction of the dynamics of rocky reef communities in eastern Tasmania. From qualitative modelling of community feedback (Marzloff et al., 2011*a*; Chapter 2) to simulations with a parsimonious mean field model of the local dynamics of Tasmanian rocky reefs, key results highlight the need for the Tasmanian rock lobster fishery to move towards an ecosystem-based management that accounts for the important ecological service provided by lobsters in mitigating the effects of sea urchin destructive grazing of seaweed beds. Here the findings of this work are discussed in four sections.

(i) The first considers the value of each modelling approach in improving understanding and prediction of shifts between alternative community states in ecological dynamics.

(ii) In the second section we argue that, when considered together, the spectrum of different models we used, from qualitative to quantitative simulation models, demonstrate valuable complementarity to test model assumptions (structure, formulation, parameterisation) and provides a predictive framework that accounts for both model uncertainty and the variability of ecological dynamics.

(iii) In the third section we highlight the important results that can contribute to sound ecosystem-based management of Tasmanian reefs and the associated rock lobster fishery,

(iv) and in the final section we discuss the ecological impacts of the climate-driven incursion of *Centrostephanus rodgersii* into Tasmanian waters in the broader context of future climate-related changes that might be anticipated in the rapidly-changing marine environment around Tasmania.

5.1 A suite of tools to understand and predict shifts between alternative community states in ecological dynamics

The common focus across the different chapters of the thesis is the development and use of models to better comprehend the dynamics of alternative community states in ecosystems in general, and in eastern Tasmanian rocky reef communities in particular. Identifying and predicting phase shifts in ecological dynamics is a major challenge for ecologists, and the models applied here inform some important aspects of the presence of alternative states in ecosystems. The complementary approaches successively (i) inform the potential for alternative states and their persistence in Tasmanian rocky reef dynamics, (ii) identify the key drivers of community dynamics and decompose the different factors facilitating both the 'forward' shift (from dense and productive seaweed beds to sea urchin barrens habitat) and the 'backward' shift, (iii) characterise important threshold points and the presence of hysteresis in community dynamics, and finally (iv) enable assessment of the effects of alternative management approaches on the long-term state of reef communities and performance of the lobster fishery.

5.1.1 Qualitative modelling, positive feedback and alternative community states

Based only on qualitative knowledge of key variables and interactions, qualitative modelling provides a mechanistic understanding of how each variable's response will be influenced by the feedback properties of a perturbed system. While positive feedback is commonly associated with the concept of alternative community states in the ecological literature, other than simple conceptual diagrams, a causal explanatory framework to formally track the effects of positive feedback on the dynamics of ecological dynamics is often lacking (Scheffer and Carpenter, 2003; Suding et al., 2004). In systems with

strong positive feedback, predictions from qualitative modelling can reveal correlations in community responses to sustained perturbations that are consistent with alternative states. In our qualitative models of Tasmanian rocky reefs, patterns in sign responses driven by the presence of positive feedback emerge in the adjoint matrices that are consistent with the alternative community states observed empirically. In considering the broad scale dynamics of Tasmanian shallow reef systems the qualitative approach identified alternative community states as dense seaweed beds supporting high abundance of lobsters or, a sea-urchin-dominated system with greatly reduced seaweed cover and lobster populations at low levels (Johnson et al., 2005; Ling et al., 2009*a*). In focussing on the dynamics of understorey communities beneath the macroalgal canopy, perturbations facilitate the establishment of either a brown- or a pink-benthos state, where abalone are typically lacking from the brown-state, and abundant in the pink-state (Strain and Johnson, 2010).

As exemplified by abalone in the broadscale models of canopy dynamics, model groups that are indirectly influenced by the positive feedback can manifest ambiguous responses, not necessarily in phase with the alternative states. Nonetheless, a thorough analysis of the qualitative adjoint matrix of a system can help detect regular correlations in variable responses, either across a subset of long-term perturbations or a subset of modelled variables. The sets of variables or species that react in phase with alternative community states are of particular interest for ecosystem monitoring and intervention. Thus, qualitative modelling helped to identify the most appropriate variables to reliably track the state of rocky reef communities with regards to sea urchin destructive grazing and on which to focus further quantitative modelling, i.e. they were the three key groups (seaweed assemblage, rock lobster and the sea urchins) involved in the positive feedback driving either the shift from high seaweed cover to sea urchin barrens habitat, or the reverse shift. While demonstration of dominant positive feedback in system dynamics does not constitute absolute proof of alternative persistent states (Scheffer et al., 2001) it nonetheless identifies a strong potential for it. Given the particular difficulties of managing a system in which there exists potential for alternative persistent states and hysteresis, and the heady consequences of phase shift, qualitative modelling is helpful in that it can quickly inform managers of the need for a precautionary approach without the need to develop more complex fully quantitative models which usually require many person-years of expensive empirical effort to parameterise. The qualitative modelling is also useful in identifying the need for dedicated manipulative experiments and/or quantitative

modelling to more thoroughly investigate the presence of alternative community states. The approach can also inform about the relative balance between positive and negative feedback necessary for a system to display alternative states.

However, qualitative modelling is limited in what it can show about phase shifts between alternative states, and should be seen as complementary to field experiments or specific quantitative models (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Field experiments or quantitative models are required to characterise the nature of the shift, confirm the existence of alternative states, and identify key thresholds in system dynamics (Scheffer et al., 2001). Nonetheless, the important points are that qualitative modelling (1) can be meaningfully undertaken with basic information about links in a system and before detailed and expensive parameterisation is pursued, and (2) can detect the potential for alternative states in ecosystem dynamics and thus flag the need for a precautionary approach in managing human activities in a system until community dynamics are more specifically and thoroughly investigated.

5.1.2 Calibration and sensitivity analysis of a model with alternative states

While they may be seen as useful, even essential, to support informed decision-making in management, robust simulation models of ecosystems with alternative states are challenging to build and validate. When there are alternative states in model dynamics, if follows that no trivial criteria can provide reliable metrics to assess the goodness-of-fit of such models. Chapter 3 presents a simulation-based validation and analysis of model sensitivity to input parameters of TRITON, the quantitative simulation model developed specifically to study phase shifts between alternative community states in lobster-sea urchin-seaweed dynamics. Pattern-oriented modelling, i.e. comparing patterns emerging from Monte-Carlo simulations of model dynamics with large-scale empirical observations provides a useful approach to calibration (Grimm et al., 2005) and, to a large extent can be accepted as validating the broad-scale dynamics of TRITON.

Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test (Saltelli et al., 1999), we were able to rank the influence of key parameters on model behaviour. Through a set of independent sensitivity tests, the approach to first focus on the model's overall dynamics, and then decompose total model behaviour

into the individual features that characterised the 'forward' and reverse shifts (van Nes and Scheffer, 2003) was powerful and informative. Rather than using one single global sensitivity test, the set of sensitivity tests provides a comprehensive analysis of the shift between alternative community states in the model. The simulations underlying the sensitivity tests also inform parameter influence on transition times in the model for shifts from one state to the other.

5.1.3 Simulation-based exploration of phase shift in modelled community dynamics, indicating thresholds and management interventions

Monte-Carlo simulation using TRITON helps tackle key questions for managing rocky reef communities in Tasmania by characterising key thresholds. These tipping points define important reference points (e.g. ∼6200 g of lobster. $200m^{-2}$ as the biomass density associated with a 5% chance of barren forming) to mitigate the risk of sea urchin destructive grazing. They also reflect a hysteresis in modelled community dynamics as evidenced by different thresholds associated with the 'forward' and the 'backward' shifts. Note, however, that because of spatial heterogeneity in ecological dynamics, captured in TRITON through Monte-Carlo simulations, no definite and precise threshold values can define the tipping points in the dynamics of a given ecosystem. If thresholds in ecological dynamics are challenging (Briske et al., 2010; Samhouri et al., 2010; McClanahan et al., 2011), but not impossible (Carpenter et al., 2011), to identify empirically, Chapter 4 suggests that tipping points are not that trivial to apprehend using simulation models. Generalised linear models can identify model groups that best relate to the likelihood of model shift and provide a robust framework to determine threshold points associated with a given level of risk that managers or industry are willing to take. However, community thresholds identified in terms of biomass densities on a local reef (∼100 m^2 to 10 ha) are not straightforward to transpose at the regional scale of fishery management in Tasmania (∼100 km). While estimates of community thresholds cannot directly informed definite target points for current lobster fishery management, Chapter 4 highlights the need for management objectives to minimise the risk of sea urchin grazing. The same Monte-Carlo simulation provides a valuable assessment of the tradeoffs between long-term ecological outcomes and fishery productivity under alternative management interventions. The discrepancies between simulations with TRITON and with the single-species stock assessment model for the rock lobster fishery reveal the need for fishery management to

move towards an ecosystem-based approach to account for the key ecological role of rock lobster on Tasmanian rocky reefs.

This thesis illustrates the crucial role that modelling (i.e. qualitative, quantitative or simulation-based assessment of model sensitivity to parameter) can play in better appreciating and understanding alternative community states in ecological dynamics. The models are fundamentally useful to (i) detect the potential for alternative persistent states in reef dynamics from ecosystem feedback properties (providing critical information for managers), (ii) identify the existence of different ecologies and drivers of community dynamics in both the barrens and seaweed-dominated states, (iii) estimate of thresholds in reef dynamics, and (iv) assess the effects of management measures on ecosystem state. The results show clearly that qualitative modelling, the sensitivity analyses of TRITON to input parameters, and results from Monte-Carlo simulations, each contributes original and critical information about alternative states and hysteresis in community dynamics. The modelling is useful in complementing existing knowledge from field observations and empirical experiments. It is an important result that the modelling approaches show complementarity and help to both develop a more comprehensive picture of the potential for alternative states on Tasmanian rocky reef dynamics and to inform management about choices in management responses.

5.2 Assessing model robustness and enveloping uncertainty in model predictions

To provide reliable information and support natural resource management, an ecological model requires both comprehensive testing of in-built assumptions and validation against available information on observed dynamics.

5.2.1 Qualitative Modelling to assess structural uncertainty

Testing for uncertainty in ecological models often focuses on sensitivity analysis of parameter values (Saltelli et al., 2000) while the question of uncertainty in model structure usually remains underestimated at best, or is unaddressed entirely (Laskey, 1996; Dambacher and Ramos-Jiliberto, 2007; Hosack et al., 2008). Chapter 2 emphasises the importance of assessing structural uncertainty in models of complex systems, especially in

ecological models where the understanding of system interactions is typically incomplete. In the same sense that testing model sensitivity to parameter values is essential (Saltelli et al., 2000), questioning the qualitative information (e.g. about ecological interactions) used to build models is essential in testing assumptions about the model structure itself (Hosack et al., 2008). Qualitative modelling of feedback properties is well suited to assess structural uncertainty in models of complex systems (Hosack et al., 2008; Metcalf et al., 2008; Hosack et al., 2009). This approach enabled identifying the most parsimonious model structure to address the ecological effects of sea urchin destructive grazing (i.e. the need to include the minimum components of seaweeds, sea urchins and lobsters), and to assess options for management intervention.

5.2.2 Uncertainty in model formulation and parameterisation

Robust model parameterisation is key to any useful simulation framework and represents a major effort behind the development of the TRITON model (Appendix 3B). Even for the best-studied ecosystems, where observational or experimental data can support detailed model parameterisation, quantification of ecological processes is uncertain (Novak and Wootton, 2008), and so testing for model sensitivity to parameter values constitutes an essential ingredient of ecological modelling (Saltelli et al., 2000). Through a set of independent sensitivity tests (Saltelli et al., 1999), model dynamics can be analysed as a whole and decomposed to develop a comprehensive understanding of the key drivers, and assess. While sensitivity analyses based upon each model group can be informative, considering the overall community structure described by the first axis of the PCA on normalised outputs of the different model groups provide a reliable one-dimensional summary to assess sensitivity of model behaviour without having to screen each and every model group.

Pattern-oriented modelling (Grimm et al., 2005) offers a valuable approach to assess and calibrate the dynamics of a model with alternative states in circumstances where no objective quantitative validation criteria can easily be defined. Comparing patterns emerging from Monte-Carlo simulations with large-scale observations of Tasmanian reef communities helped to restrict values of sea urchin recruitment rates to a realistic range so that TRITON behaves as observed on rocky reefs in the 'real-world'.

Comprehensively testing model assumptions, whether related to model structure, formulation or parameterisation, contributed to both:

(i) a better understanding of the key drivers of modelled community dynamics. Both lobster and sea urchin recruitment, and the level of lobster fishing and removal of sea urchins all emerged as important factors controlling the model's propensity to shift to sea urchin barrens. It is noteworthy that recruitment of both groups is highly dependent on large-scale oceanographic features in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011) and thus not able to be directly manipulated by human behaviour, while extraction of sea urchins and lobsters from the system is directly under human control;

(ii) and assessment of model limitations due to incomplete understanding of Tasmanian rocky-reef dynamics. Several ecological processes, which are unlikely to highly influence the broad dynamics of phase shifts, are coarsely or not explicitly captured in TRITON. In particular, the dynamics of other guilds and size groups within the seaweed bed community, the effects of storms and wave action on algal cover (Wernberg, 2005; Reed et al., 2011), and greater detail on the effect of sea urchin grazing on macroalgae (described after Hill et al. (2003) in TRITON) and of lobster predation rates on sea urchins across a range of densities of both predator and prey, would require further field observations and experiments to be finely captured in the model.

5.2.3 Accounting for space-time variability and assessing prediction uncertainty through Monte-Carlo simulations

Variability in space and time is a key feature of real ecological dynamics, and needs to be adequately captured in any realistic ecosystem model (Annan, 2001). However, seasonality and the frequency and magnitude of extreme events (i.e. storm surges) (Reed et al., 2011), which potentially play a role in sea urchin barrens formation, are not captured in TRITON because they are difficult to quantify and largely irrelevant to the long-term ecological dynamics of sea urchin destructive grazing. Due to the scarcity of information about temporal variability in most modelled process, the only source of stochasticity through

simulations in TRITON comes from interannual variability in rock lobster and sea urchin recruitment rates.

In TRITON the distribution of each model parameter was estimated using data, mostly from Tasmanian-based empirical observations and experiments. Exploration of the 90% confidence interval of each parameter estimate through hierarchical Monte-Carlo simulations (Saltelli et al., 1999) account for uncertainty both, in individual processes captured in the model, and in the overall dynamics that emerge out of the complex interactions between these processes (Laskey, 1996; Melbourne-Thomas et al., 2011*a*; Polasky et al., 2011). Indeed, each set of Monte-Carlo simulations samples any combinations of input parameters, including the most extreme ones. Thus, while environmental variability through space (from reef to reef) is not easy to characterise, these simulations are likely to capture some of this heterogeneity in the environmental conditions found on Tasmanian rocky reef (e.g. in habitat, depth, exposure to urchin larvae, etc.). Assessing uncertainty in model predictions allows us to advise about the expected general consequences of alternative management options rather than prescribe definite recommendations for management (Francis and Shotton, 1997).

Both the qualitative and quantitative simulation modelling reveal the importance of non-trivial indirect effects (e.g. high level feedback or interactions between modelled processes) to the modelled community dynamics. Indeed, while qualitative modelling can track the influence of indirect effects and the contribution of high-level feedback to community dynamics (Marzloff et al., 2011*a*), simulation-based sensitivity analysis suggests that the quantitative model TRITON is mostly sensitive to interactions between modelled processes rather than to direct effects of changes in input parameters. Thus, both the qualitative and quantitative modelling approaches presented in this thesis provide valuable tools to capture and emphasise the importance of indirect responses of the reef community to perturbations, and also to test the non-trivial indirect effects of management interventions and environmental changes on ecosystem state. In keeping with previous work, the dominant influence of interactions between input parameters on model dynamics that we observed is common in models of complex dynamics (Saltelli et al., 1999, 2009). More generally, this thesis highlights the value of ecological modelling to adequately assess complex non-trivial responses of ecosystems to perturbations.

5.3 Towards an ecosystem-based management for Tasmanian rocky reef fisheries

The suite of models built and tested to realistically capture alternative states in seaweed-based reef community dynamics provides valuable information towards a more integrated ecosystem-based management of Tasmanian rocky reef communities and associated fisheries. Overall, these models help detect the potential for alternative community states and identify the key mechanisms driving these shifts. More specifically, they provide a framework to apprehend threshold points in reef community dynamics and test the effects of different management strategies on long-term ecosystem state and fishery productivity.

5.3.1 Qualitative modelling and general information for an Ecosystem-Based Fishery Management

Qualitative modelling can provide valuable insight into the indirect effects of human activities on ecosystem state, and qualitative predictions can help distinguish the most useful variables for both ecosystem monitoring and management intervention (Dambacher et al., 2009; Marzloff et al., 2011*a*; Metcalf et al., 2011). In the thesis, qualitative modelling helped understand the general dynamics of Tasmanian rocky reefs and in particular the potential for alternative community states both, in lobster-sea urchin-seaweed bed dynamics, and in the dynamics of epilithic algal assemblages under the macroalgal canopy: 1) under sustained changes in environmental conditions (e.g. climate-driven increase in sea urchin recruitment) or human impacts (e.g. harvesting of rock lobster), seaweed-based reef communities are predicted to respond towards either a dense seaweed bed supporting a high abundance of lobster or, alternatively, a sea-urchin-dominated barren with reduced seaweed cover and where lobster populations decline (Johnson et al., 2005; Ling et al., 2009*a*); 2) in the dynamics of understorey algal communities, the qualitative predictions suggest that removal of abalone by fishing will locally facilitate the establishment of the brown-benthos state where abalone density virtually collapses (Strain and Johnson, In press). The brown-benthos state, characterised by a matrix of filamentous and foliose algae, semi-consolidated sediment and sessile invertebrates, can overgrow the pink-benthos state dominated by crustose red algae where abalone are abundant (Strain and Johnson, 2010).

These examples show the capacity of qualitative modelling to indicate the general ecosystem effects of fishing rock lobster and blacklip abalone and the climate-driven increase in sea urchin recruitment on the state and well-functioning of Tasmanian rocky reef communities. While useful in generally describing the community effects of fishing (Dambacher et al., 2009), qualitative modelling does not provide any specific recommendations directly relevant to fishery management.

5.3.2 Development of a parsimonious simulation model and scenario testing

The quantitative modelling extends the consideration of broad dynamics illuminated by the qualitative approach to provide more specific recommendations for the lobster fishery. First, the set of global sensitivity analysis tests reveal high contributions to variance in simulation outcomes of parameters associated with lobster fishing, and culling of sea urchins. Along with lobster and sea urchin recruitment rates, harvesting of lobsters and sea urchins highly influences the model's ability to shift from dense seaweed cover to sea urchin barrens habitat, or the capacity for seaweeds to recover on sea urchin barrens, and so harvesting rates emerge as more effective management levers than implementation of a maximum legal size alone. The time for the model to shift from one state to the other is of the order of two to three decades, so it is therefore prudent that management focuses on the prevention of barrens formation rather than on restoration strategies that are unrealistic to implement over lengthy time frames (i.e. decades rather than a few years, which is the time scale of most management plans).

Finally, Chapter 4 provides information for current managers to better account for the important ecological role or 'service' that lobsters provide to Tasmanian rocky reef communities. Estimates of key thresholds in Tasmanian reef communities, which can constitute important reference points to mitigate the effects of sea urchin destructive grazing (e.g. $\sim$6200 g of lobster. $200m^{-2}$ as the biomass density associated with a 5% chance of barren forming), clearly identify a hysteresis in modelled community dynamics. This hysteresis highlights the need for management to focus on preventing the formation of sea urchin barren rather than on the far more challenging restoration of seaweed beds once extensive barren habitat has established.

When examining thresholds in modelled community dynamics, let us keep in mind that absolute model predictions always need to be considered with caution. It is well-accepted

that due to model uncertainty, quantitative model predictions should advise about the expected general consequences of alternative management options rather than prescribe definite absolute recommendations for management (Francis and Shotton, 1997): the precision and the accuracy of absolute predictions from complex ecological models depend on the reliability of all input parameters, hence simulation outcomes are often interpreted in relative terms (e.g. comparisons among alternative scenarios; Smith et al., 2011) rather than as absolute predictions. However, absolute estimates of thresholds in community dynamics are essential to a sound management of Tasmanian rocky reef community, and if managers do not have access to the best absolute estimates that researchers can provide, even with all their caveats, they will make management decisions anyway. The simulations with TRITON, based upon the best available information about Tasmanian reef ecology, currently provide the most reliable and conservative estimates of thresholds in reef community dynamics: indeed, all model parameters were estimated using the latest and most comprehensive sources about Tasmanian rocky reef ecology, so estimates from simulations with TRITON summarise the best currently available knowledge to inform management. Note also that to tackle uncertainty in model prediction, parameter uncertainty has been addressed in both chapters 3 and 4: model sensitivity to input parameters was investigated comprehensively in Chapter 3, while the results presented in chapter 4 are from thousands of Monte-Carlo simulations to fully sample parameter space and account for parameter uncertainty in model predictions. Nonetheless there remains, of course, uncertainty in some assumptions and processes behind the TRITON model. However, decisions while developing the model were always made conservatively. As a consequence, absolute model predictions (and simulation-based estimates of threshold in community dynamics) are conservative in terms of estimating the risk of sea urchin destructive grazing of Tasmanian seaweed beds.

Direct culling of sea urchins together with a reduced harvest of lobsters is the most effective ecological intervention to minimise the impact of *C. rodgersii* grazing on Tasmanian reefs. The dual actions of reducing removal of lobsters and increasing removal of sea urchins is notably more effective than measures aimed solely at building lobster populations (e.g. reduction in lobster fishing or implementation of a maximum legal catch size). An important result of the modelling is that a maximum sustainable yield estimated from the single species stock assessment model does not account for the ecosystem service delivered by larger lobsters. Current management overlooks the potential for some form

of depensation effect in lobster population dynamics, i.e. the decrease in recruitment due to the loss of seaweed habitat following sea urchin destructive grazing at low density of large rock lobsters. In this context, this thesis emphasises the need for an ecosystem-based management approach for the Tasmanian rock lobster fishery. While highlighting the need for fishery management to better account for the ecological role of lobster in Tasmanian rocky reef communities and revise key target points accordingly, the range of model simulations provide a valuable assessment of the tradeoffs in terms of both long-term ecological outcomes and fishery productivity associated with alternative management interventions.

5.3.3 Mismatch between the scale of rocky reef dynamics and fishery management

Simulation models constitute useful support tools to manage natural resources, especially as the consequences of alternative regulations or management scenarios are difficult if not impossible to assess experimentally at the spatial and temporal scales of ecological dynamics (e.g. Melbourne-Thomas et al., 2010, 2011*b*). However, in eastern Tasmania commercial fisheries are managed at the scale of regional 'blocks' (scale of 10^3 m), while sea urchins can deplete seaweed beds, create and maintain extensive 'barren' areas at the scale of individual reefs (scales of 10^2 - 10^3 m). While it is clear that *C. rodgersii* represents one of the major threats for Tasmania's subtidal rocky-communities and coastal fisheries (Johnson et al., 2005), a decision-support tool that adequately addresses both the spatial dynamics of sea urchin barrens formation and the effects of lobster fishing and fisheries regulations on the state of reef communities, is currently lacking. Such a tool, structured as a connected network of local models in which each represents the dynamics of individual reefs, is under development to support the management of rocky-reef communities at the scale of the entire east coast of Tasmania (Marzloff et al., 2011*b*). The regional dynamics in the model emerge from the combination of these local dynamics and dispersal of larvae between reef patches. Regional connectivity between reefs is derived from a particle-tracking model based upon patterns of surface circulation (Condie et al., 2005). This framework will to some extent bridge the current gap between the findings presented in this thesis about the dynamics of sea urchin destructive grazing at the scale of individual patches of reef (e.g. threshold points expressed a biomass density of rock lobster, defined in $g.200m^{-2}$), and actual regional management of the Tasmanian rock lobster fishery

(under regional catch quotas, defined in Kt for management blocks covering large stretch of coastline). This mismatch between the scale of ecological dynamics and the scale of fishery management currently constitutes a major challenge for the implementation of sound ecologically sustainable management decisions for Tasmanian rocky reef communities.

5.4 Challenges to adapt to climate-driven changes in Tasmanian marine ecosystems around Tasmania

Under climate-driven large-scale changes in global ocean circulation, southeastern Australia, including eastern Tasmania, has been identified as a regional 'hotspot' with the ocean warming about three to four times faster than the global average (Holbrook and Bindoff, 1997; Ridgway, 2007*a*). In particular, the warm nutrient-poor tropical East Australian Current, which sweeps southwards along the East coast of Australia, is intensifying as part of large scale changes to the South Pacific Gyre (Ridgway, 2007*b*). The list of known and potential changes to the Tasmanian marine environment associated with these changes in larger-scale oceanographic features is long and expanding (Johnson et al., 2011). Notably, sea urchin and southern rock lobster recruitment processes in eastern Tasmania, both highly influential parameters underpinning the dynamics of TRITON, are largely determined by large-scale climate-driven oceanographic features (Banks et al., 2007; Bruce et al., 2007; Ling et al., 2009*b*; Johnson et al., 2011). Like many other species migrating poleward from Australia's mainland coast to Tasmanian waters (Redmap, 2010; Johnson et al., 2011), the long-spined sea urchin is now fully established, viable and, in some areas of northeast Tasmania, the dominant species on shallow reefs (Johnson et al., 2005, 2011). Populations of the sea urchin are constantly expanding, both in abundance and in space along the east coast of Tasmania (Ling, 2008; Ling et al., 2009*b*). Conversely, in eastern Tasmania there is some evidence that southern rock lobster larvae, ostensibly supplied from Victorian and possibly South Australian populations (Bruce et al., 2007), and lobster recruitment have declined over the last five to six years with the intensification of the East Australian Current (Johnson et al., 2011), although the trend is far from established. Accordingly, most long-term projections for southern rock lobster assumed more frequent failures in annual recruitment and predict a decline in populations in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011). While in the coming decades Tasmanian reef communities may see a partial substitution of southern rock lobster with their more northern counterpart, the eastern rock lobster (*Sagmariasus verreauxi*), precise predictions

of shifts in species distribution and abundance are lacking and these climate-driven changes can only be described in broad qualitative terms.

C. rodgersii barrens currently constitute a pressing concern for managers of reef communities and fisheries in Tasmania (Johnson et al., 2005; Pecl et al., 2009; Johnson et al., 2011). However, *C. rodgersii* is just one species among many others expanding their range to establish populations in Tasmania (Redmap, 2010), but whose ecosystem impacts are unknown. In the coming decades, climate-driven changes are likely to bring more surprises to Tasmanian rocky reefs, and challenging surprises for associated fisheries and their managers. The expected changes to come have the capacity to affect virtually every physical attribute of marine ecosystems in the Tasman Sea from nutrient load, temperature, salinity and pH, to biological components including plankton, seaweeds, other components of benthic communities, and ecosystems supporting pelagic fishes (Johnson et al., 2011).

Appendix

A Derivation of parameter estimates for the local TRITON (Temperate Rocky reef communities In Tasmania with lObsters and urchiNs) model

A.1 Introduction

A.1.1 Context of the model: units, temporal and spatial scales

The variables in this local model of Temperate Rocky reef communities In Tasmania with lObsters and urchiNs (TRITON) are expressed in biomass density (g.200 m^{-2}). The default parameterisation corresponds to a 200 m^2 reef area, as both a coherent spatial scale on which to capture reef community dynamics and the most common scale used for underwater surveys and experiments available to inform model dynamics. Biomass is given as wet weight, which is often directly available from experiments or technical reports and represents an ecologically sound unit for trophic interactions (e.g. Christensen and Walters (2004)). Rates of change, defining population dynamics and trophic interactions, are given as annual.

For each parameter, we define a mean estimate as well as a probability distribution (e.g. uniform with a minimum and maximum bounds or normal with mean and standard error) to account for parameter uncertainty through Monte-Carlo simulations (e.g. Saltelli et al. (1999)).

A.1.2 Functional groups

The number of groups and/or species in the model is kept to a minimum (seaweed assemblage, sea urchin, rock lobster; see chapter 3) so as to focus on the impact of grazing by the invasive long-spined sea urchin *Centrostephanus rodgersii* on Tasmanian subtidal reef communities (Marzloff et al., 2011*a*). The model explicitly includes southern rock lobster, the main predator of the sea urchin in Tasmanian waters, to assess the community effects of alternative management strategies for this key Tasmanian fishery.

A.1.3 Appendix structure

This appendix details the parameterisation of all the processes explicitly modelled in TRITON and is organised in four main sections: (A.2) population dynamics of each of the three groups; (A.3) trophic interactions; (A.4) model closure and factors implicitly accounted for in TRITON; (A.5) Limitations and guidance for future research.

A.2 Population dynamics

A.2.1 Logistic population dynamics

Population dynamics following a logistic growth function can be expressed as:

$$\frac{dB}{dt} = \alpha B \left[\frac{K - B}{K}\right], \tag{A.1}$$

with B, biomass density (g. 200 m^{-2}); K, carrying capacity (g. 200 m^{-2}); α, intrinsic growth rate ($year^{-1}$); t, time expressed in year.

Defining logistic population dynamics

The following equation defines an analytical solution to Eq. A.1 (Kot, 2001):

$$B(t) = \frac{K}{1 + \beta \exp(-\alpha\, t)}, \tag{A.2}$$

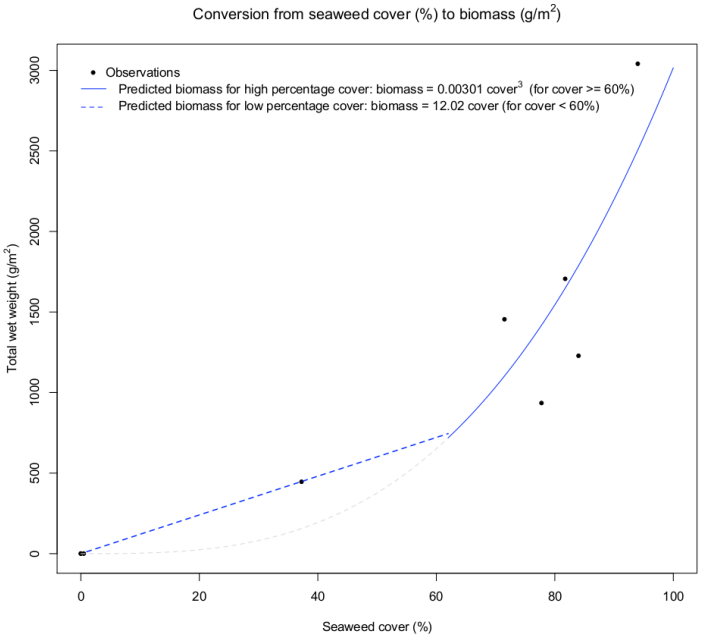
with $\beta = \frac{K - B_0}{B_0}$, where B_0 is the initial biomass density at time t=0.

Using observations of population biomass density through time (e.g. Fig.A.2 for the seaweed bed) standardised to a 200 m^2 area, the intrinsic growth rate α, the carrying capacity K and the constant β from Eq. A.2 were estimated using the non-linear least square function *nls* of the R language for statistical computing, version 2.12 (R Development Core Team, 2010).

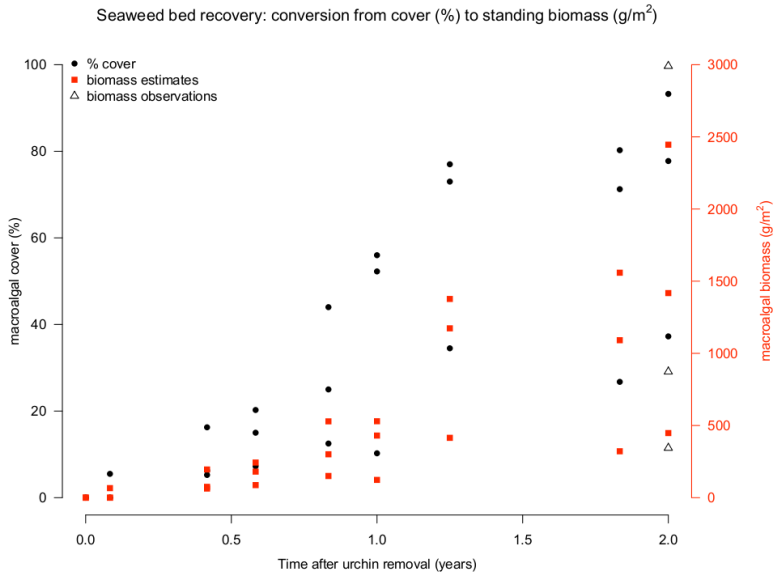
Seaweed bed logistic growth

Data Seaweed bed dynamics was defined based on data of seaweed bed recovery following the removal of grazers (Ling, 2008). The first step involved translating these data reported in percentage cover into wet biomass density of the seaweed bed (see Fig.A.1).

Parameter estimates Note that in one of the 3 experimental sites the seaweed bed did not significantly recover for various reasons (shade and unsuitable reef properties; S.D. Ling, personal communication). This site was ignored when fitting the logistic growth function (Fig.A.2). Parameter estimates for seaweed bed logistic dynamics (Eq.A.2) are given in Table A.1.



a)



b)

Figure A.1: a) Conversion from percentage cover (%) to biomass density (g.m^{-2}) for Tasmanian seaweed beds (*Ecklonia radiata, Phyllospora comosa*; Ling, unpublished data). b) Seaweed bed recovery data from Ling et al (2008), aggregated across quadrats for 3 experimental sites. The data originally in percentage cover (in %; black dots) were converted to biomass density (in g.m^{-2}; red squares).

Table A.1: Parameter estimates for the seaweed bed logistic growth function (Eq.A.2).

	Estimate	Standard error	t value	$Pr(>\|t\|)$
α_{SW}	4.43	1.65	2.690	0.0168
β_{SW}	1.35e+02	2.18e+02	0.621	0.5439
K_{SW}	3.4e+05	3.6e+04	9.488	9.94e-08

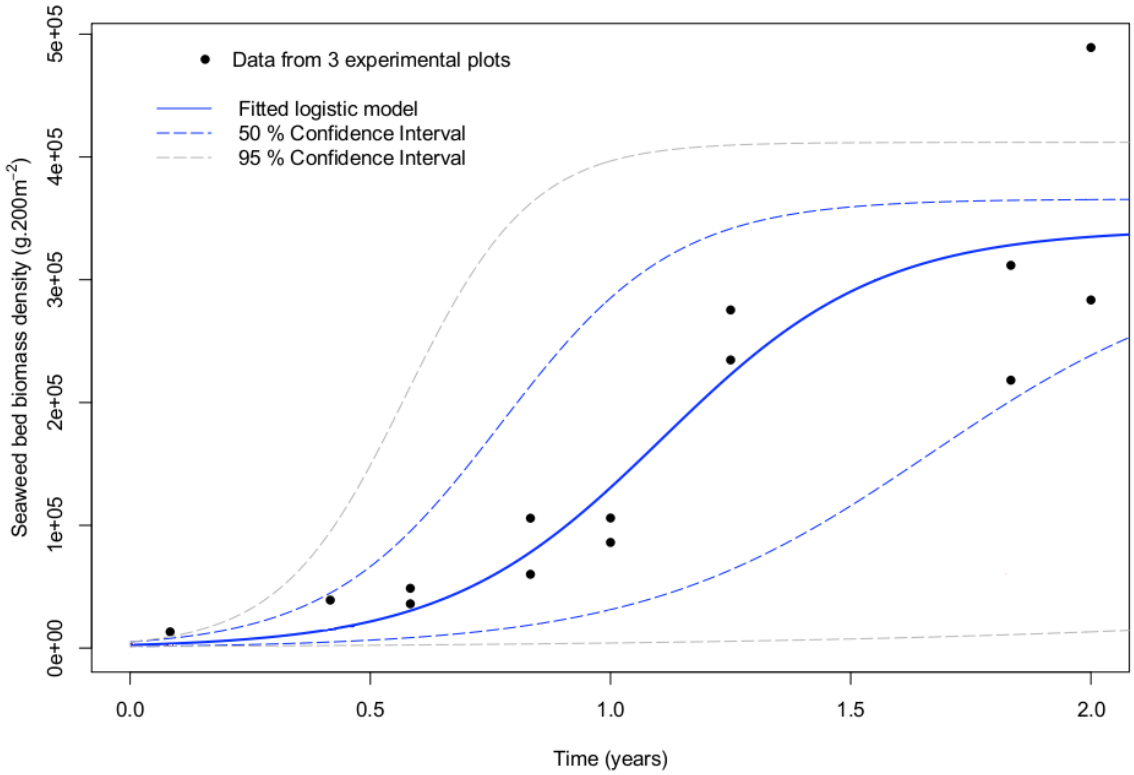


Figure A.2: Logistic growth model (with 50 and 95% confidence intervals) fitted to data of seaweed bed recovery following urchin removal (Ling, 2008). Light conditions and marginal habitat features did not allow the seaweed bed to recover at one of the three sites, which was excluded from this analysis. Depth: 9-15 m.

Limitations and other references Intrinsic growth rate for various temperate seaweed species are reported to vary from c. 4 to 7 year^{-1} under optimal conditions (Mohn and Miller, 1987; Lobban and Harrison, 1996).

Carrying capacity of temperate seaweed beds, i.e. maximum biomass density, can vary significantly depending on light (depth), exposure to swell, temperature and algal composition. Our estimate of maximum biomass density (wet weight) falls within the low range of reported values for carrying capacity of temperate seaweed beds: 4 kg kelp.m^{-2} in

Nova Scotia (Lauzon-Guay et al., 2009); 6-18 kg.m^{-2} for *Ecklonia radiata* beds in Western Australia (Kirkman, 1984).

In Tasmanian waters, *E. radiata* beds are the most at risk of destructive grazing by *C. rodgersii*. Several studies have measured individual *E. radiata* plant growth and productivity (Kirkman, 1984, 1989; Sanderson, 1990). *E. radiata* plant growth is often compared to a conveyor belt of tissue moving from the meristematic region near the stipe of the plant towards the extremity of the blades where it erodes (Sanderson, 1990). If both tissue production and erosion can be measured for *E. radiata* seaweed beds, the effects of urchin grazing on individual macroalgae is poorly known so this information available about the dynamics of individual macroalgae was not directly usable in TRITON. Additionally, other processes (e.g. wave action especially during storms) are not accounted for explicitly in the model. These processes can potentially erode macroalgal plants as much as sea urchin grazing (Reed et al., 2011). Seaweed bed dynamics and sea urchin grazing on macroalgae in particular would require some dedicated field experiments in the future to better represent sea urchin destructive grazing in the model.

Urchin logistic growth

Data The long-spined sea urchin has progressively extended its natural range southwards along the east coast of Tasmania over the last decades. *C. rodgersii* has progressively settled through time in Tasmania along a north-south gradient. From large-scale surveys of *C. rodgersii* population size-structure along the East coast of Tasmania (Johnson et al., 2005; Ling and Johnson, 2009), information about sea urchin population age and biomass density could be derived at different sample sites to describe population growth (Fig.A.3). Substituting space for time, this data provides information about urchin population dynamics (biomass building following first settlement). The 90% quantile of population age distribution is used as an estimate of the elapsed time since first settlement of *C. rodgersii* at a given site.

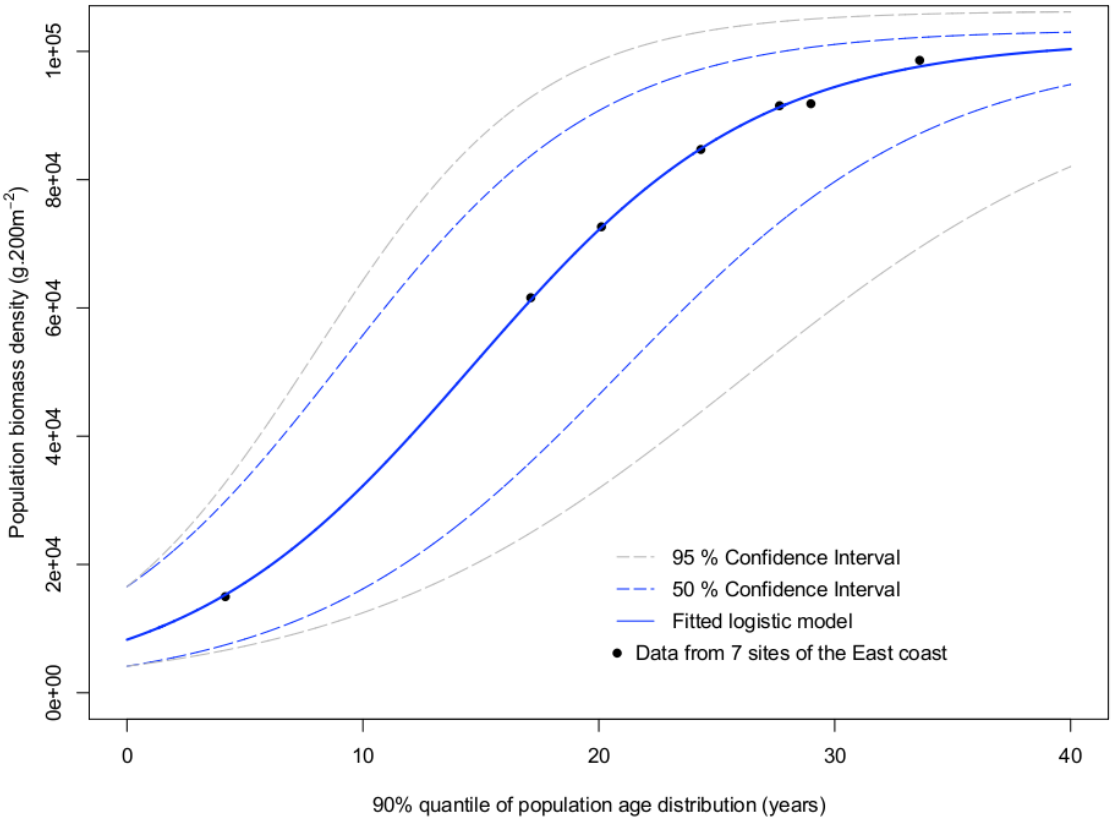


Figure A.3: Logistic growth model (with 50% and 95% confidence intervals) fitted to data from large-scale survey of *C. rodgersii* population on the east coast of Tasmania (Johnson et al., 2005; Ling and Johnson, 2009). The 90% quantile of population age distribution is used as a proxy for the time elapsed since first settlement of the urchin.

Rock lobster logistic growth

Data The Maria Island and Tinderbox marine reserves were implemented in 1991 and reef communities within the reserve have been monitored regularly following protection from fishing (Barrett et al., 2007; Edgar et al., 2009). Biomass density of lobster through time in these two reserves (Fig.A.4) is derived from size-structured survey of invertebrate abundance using the following length-weight relationship for southern rock lobster (*Jasus edwardsii*): $B = 0.000271\, L^{3.135}$ (Punt and Kennedy, 1997) relating individual lobster biomass (B) in grams to carapace length (L) in mm.

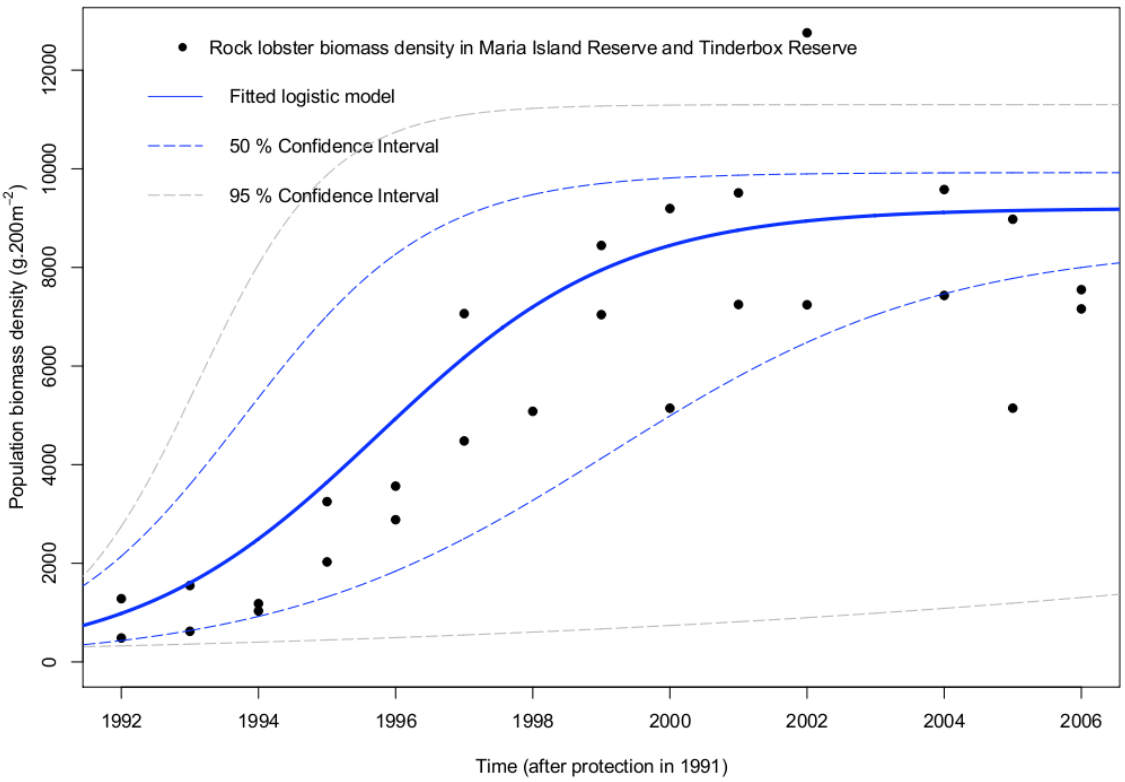


Figure A.4: Logistic growth model (with 95% confidence intervals) fitted to data from surveys of rock lobster mean biomass density in Maria Island and Tinderbox marine reserves following protection in 1991 (Barrett et al., 2007; Edgar et al., 2009)

A.2.2 Size-structured population dynamics

Both sea urchin and rock lobster dynamics are size-structured in TRITON. Thus, while figures A.3 and A.4 present the data used to fit sea urchin and rock lobster population dynamics, the following section provides the estimates of the parameters defining sea urchin and rock lobster population dynamics in the model. Size-structured population dynamics are defined for rock lobster and sea urchin populations based upon information about individual growth function (size-dependent mean and standard deviation of growth increment) and natural mortality rates (e.g. Punt and Kennedy, 1997). Length-weight relationships were required to convert from abundance to biomass to accomodate our biomass-based modelling approach.

Defining size-structured population dynamics

A size-structured population model with n size classes can be written for any class s as:

$$B_{s,t+1} = B_{s,t} \times \exp(-\beta) + \sum_{j=0}^{s} \left[\delta'_{s,j} B_{j,t}\right] - \sum_{i=s+1}^{n} \left[\delta_{i,s}\right] B_{s,t} \ (+r_t, \textit{ if: } s = 1) \qquad \text{(A.3)}$$

with $B_{s,t}$, biomass density of size class s at time t (g.200 m^{-2}); $\delta'_{i,j}$, biomass-based transition probability from size class j to i, (element of the i-th row, j-th column of the transition probability matrix; in $year^{-1}$); $\delta_{i,j}$, abundance-based transition probability from size class j to i (year-1); β, natural mortality ($year^{-1}$); r_t, recruitment rate into the first size class at time t (g.200 $m^{-2}.year^{-1}$). The size-structured population model relies on a transition probability matrix representing biomass fluxes between size classes. Size-structured population dynamics is defined following a stepwise process: 1) definition of recruitment variability (parameterisation of a stochastic function); 2) definition of the growth transition probability matrix; and 3) estimating mean recruitment rate and natural mortality by fitting simulated size-structured dynamics to available data.

Recruitment stochastic function Recruitment to the first size class is expressed as an additive stochastic term. Interannual variability in the magnitude of recruitment can be adequately represented using a lognormal stochastic function (M. Haddon, pers. comm.; see Eq.A.4). Lognormal stochastic recruitment rate at time t can be written as:

$$r_t = \mu \exp(\gamma + \sigma \times \epsilon) \qquad \text{(A.4)}$$

with μ, mean recruitment rate (g.200 $m^{-2}.year^{-1}$); γ and σ, mean and standard deviation of the lognormal stochastic function defining the magnitude of interannual recruitment variability; ϵ, a random term following a normal distribution of mean 0 and standard deviation of 1; γ and σ can be derived from the mean m and the variance v of the observed lognormally-distributed variable as: $\gamma = log(m^2)/\sqrt{v + m^2}$ and $\sigma = \sqrt{\log(v/(m^2 + 1))}$. First, the standard deviation $\sqrt{v}$ of the observed lognormal distribution describing recruitment variability is informed using available time series, literature or expert opinion so as to derive γ and σ. We assume a mean m of 1 to centre the stochastic function on the statistically-estimated value of μ. Then, the mean annual recruitment rate μ and the natural mortality rate β are statistically estimated to optimise the fit of size-structured dynamics model against observations (Fig. A.3 and A.4).

Growth transition probability matrix Transition probability matrices are derived from individual growth functions describing size-specific growth increments (Punt and Kennedy, 1997). By definition, the matrices are abundance-based, i.e. apply to number of individuals present in each size class. Individual elements of the transition probability matrix ($\delta_{i,j}$ from Eq.A.3) are defined as:

$$\delta_{i,j} = \begin{cases} 0 & \text{if: } i < j \\ Pr\left(L_j + \Delta_j \in \left]L_i - \frac{c}{2}; L_i + \frac{c}{2}\right]\right) & \text{if: } i \text{¿= } j \end{cases} \quad (A.5)$$

with $\delta_{\mathrm{i,j}}$, abundance-based transition probability from size class j to i (year^{-1}); $\mathrm{L_i}$, mean individual length in size class i (mm); $\Delta \mathrm{L_i}$, annual growth increment in size class i follows a normal distribution with mean and standard deviation derived from the individual growth function (mm.year^{-1}); c, width of each model size class (mm). To account for individual body growth in biomass, we represent incoming biomass from size class j to size class i using a biomass-based transition probability defined as $\delta'_{i,j} = \delta_{i,j} \times \frac{b_i}{b_j}$ with $\delta'_{\mathrm{i,j}}$, biomass-based transition probability from size class j to i (year$_{-1}$); $\delta_{\mathrm{i,j}}$, abundance-based transition probability from size class j to i (year^{-1}); $\mathrm{b_i}$ and $\mathrm{b_j}$, mean individual biomasses in size classes i and j, respectively.

Mean recruitment and natural mortality rates The size-structured population dynamics model (Eq.A.3) is finally fitted to time series of species biomass density in order to estimate the most likely set of recruitment and natural mortality rates. The range of values explored is derived from literature for the natural mortality rate and from parameter estimates of fitted logistic model for the mean recruitment rate. The natural mortality rate β essentially influences the transfer efficiency of biomass from small into large size classes, while the mean recruitment rate μ regulates biomass influx into the first size class, hence restricting the maximum biomass density of the population (i.e. carrying capacity). Model residuals can be computed against each observation of biomass density at a given time t. A sum of squares of these residuals is estimated for each Monte-Carlo simulation and used as a measure of model likelihood.

Urchin size-structured dynamics

Variability in *C. rodgersii* annual recruitment on the East coast of Tasmania The early stages of *C. rodgersii* larvae can only develop if water temperature is above

12°C (Ling et al., 2008). Therefore, mean sea surface temperature in late winter (when sea urchin larvae disperse and settle) provides a good proxy for the likelihood of good recruitment. Time series (1970-2007) of sea surface temperature in Maria Island were used to characterise the frequency of annual recruitment events on the east coast of Tasmania for the recent decades (Fig.A.5). A binomial function brings stochasticity to sea urchin annual recruitment with a 0.4 probability of successful recruitment any given year (proportion of winters with sea surface temperature above 12°C; see Fig.A.5).

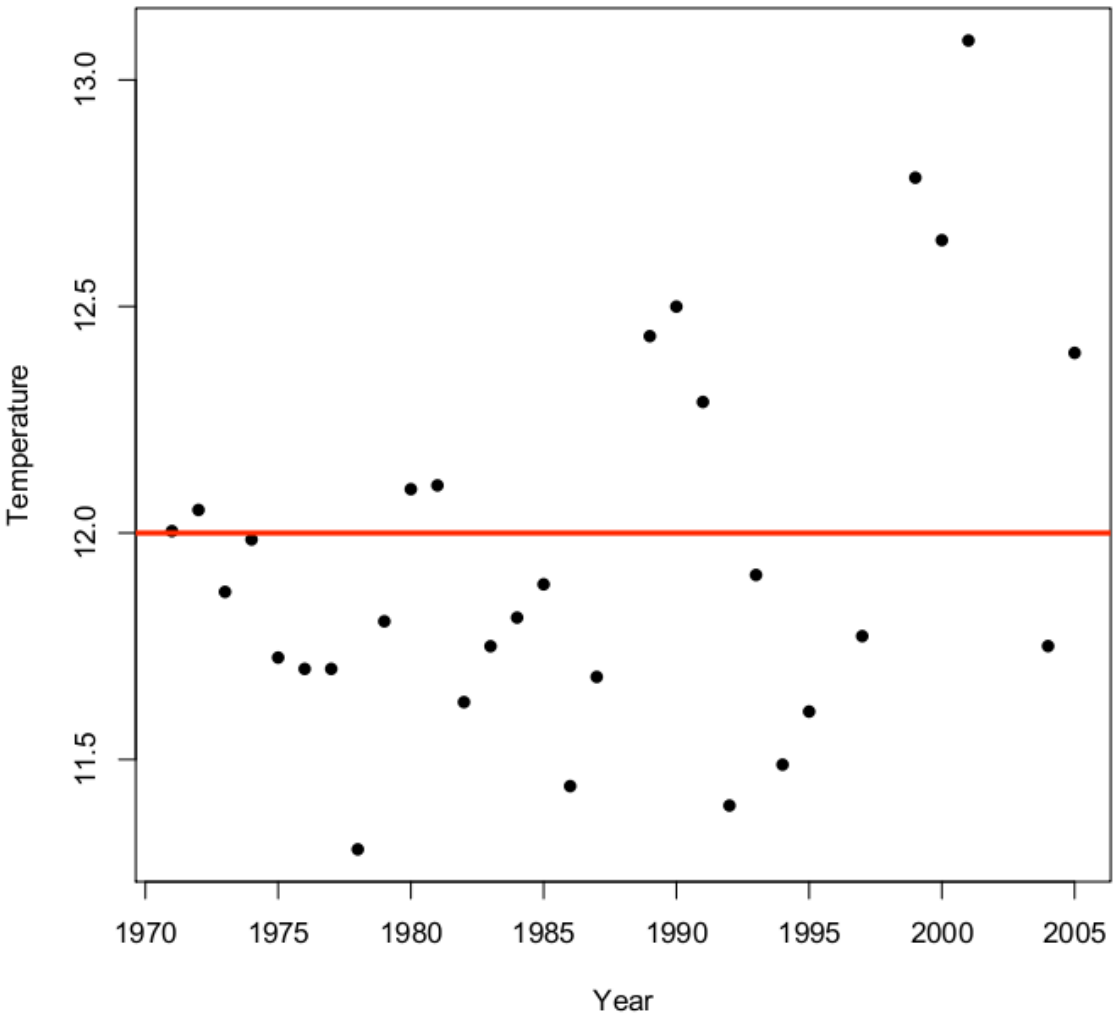


Figure A.5: Time line of mean sea surface temperature at Maria Island during winter months (August-September, i.e. time of spawning for *C. rodgersii*). The red line represents the 12°C threshold for urchin larvae to develop.

A lognormal stochastic function ($\gamma_{CR} = -0.15$; $\sigma_{CR}= 0.5$) is applied to scale the magnitude of annual recruitment rate in successful years. It captures the remaining inter-

annual variability in recruitment to the first size class in the model (which depends on both larval settlement and juvenile survival). No specific records of variability in sea urchin annual recruitment exists in Tasmania, so the lognormal stochastic recruitment function was defined to mimic the frequency of good recruitment years indicated from field observations (about 1 or 2 good recruitment events per decade; Andrew and Underwood, 1989; CR Johnson and SD Ling, pers. comm.) and information for other urchin species (Hernandez et al., 2010).

Growth transition probability matrix The transition probability matrix is derived from a generalised inverse logistic growth model for *C. rodgersii* in fringe macroalgal habitat (Ling and Johnson, 2009). Ling and Johnson (2009) fitted a generalised growth function to describe *C. rodgersii* growth increment in jaw length ΔL as a function of jaw length L_t at time t, as follows:

$$\Delta L_t = \frac{\Delta L_{max} \times \Delta t}{1 + \exp\Big[\log(19)\frac{L_t - L_{50}^m}{L_{95}^m - L_{50}^m}\Big]} + \epsilon_{L_t} \tag{A.6}$$

with $\Delta \mathrm{L_{max}} = 2.599$, maximum annual growth increment; $\mathrm{L_t}$, initial length at time t; Δt, elapsed time; $L_{50}^m = 17.994$, $L_{95}^m = 27.290$, parameters defining the shape of the inverse logistic model; $\epsilon_{\mathrm{L_t}}$, additive and normal error term of mean 0 and standard deviation $\sigma_{\mathrm{L_t}}$ defined as:

$$\sigma_{L_t} = \frac{\sigma_{max} \times \Delta t}{1 + \exp\Big[\log(19)\frac{L_t - L_{50}^m}{L_{95}^m - L_{50}^m}\Big]} \tag{A.7}$$

with σ_{max}= 0.244.

Estimating mean recruitment and natural mortality Monte-Carlo simulations with the population dynamics model were completed with sets of mortality and mean recruitment rates covering the range of possible values (natural mortality rate β_{CR} in 0.05-0.22 year^{-1}, after Lauzon-Guay et al. (2009); mean recruitment rate μ_{CR} in 1000-20000 g.200m^{-2}.year^{-1}). The goodness of fit of the size-structured population dynamics model was assessed against available data of population biomass density since time of first settlement of the urchin (see Fig.A.3; data from Ling et al., 2009*b*). Table A.2 provides the 10% most likely sets of mean recruitment and natural mortality parameters for sea urchin size-structured dynamics model. Fig.A.6 compares the distribution of sea urchin biomass

density across all size classes in simulation with observations in northeastern Tasmania on long-established barrens grounds (Ling et al., 2009*b*). Table A.2 gives the mean estimates of natural mortality and recruitment rates on which the simulated distribution is based.

Table A.2: Parameter estimates for sea urchin (*C. rodgersii*) size-structured population dynamics model (cf. Eq.A.3 and Eq.A.4).

	Unit	Mean	Range
Natural mortality β_{CR}	year^{-1}	**0.11**	0.1-0.15
Mean recruitment rate μ_{CR}	g.200m^{-2}.year^{-1}	**4100**	2500-10000

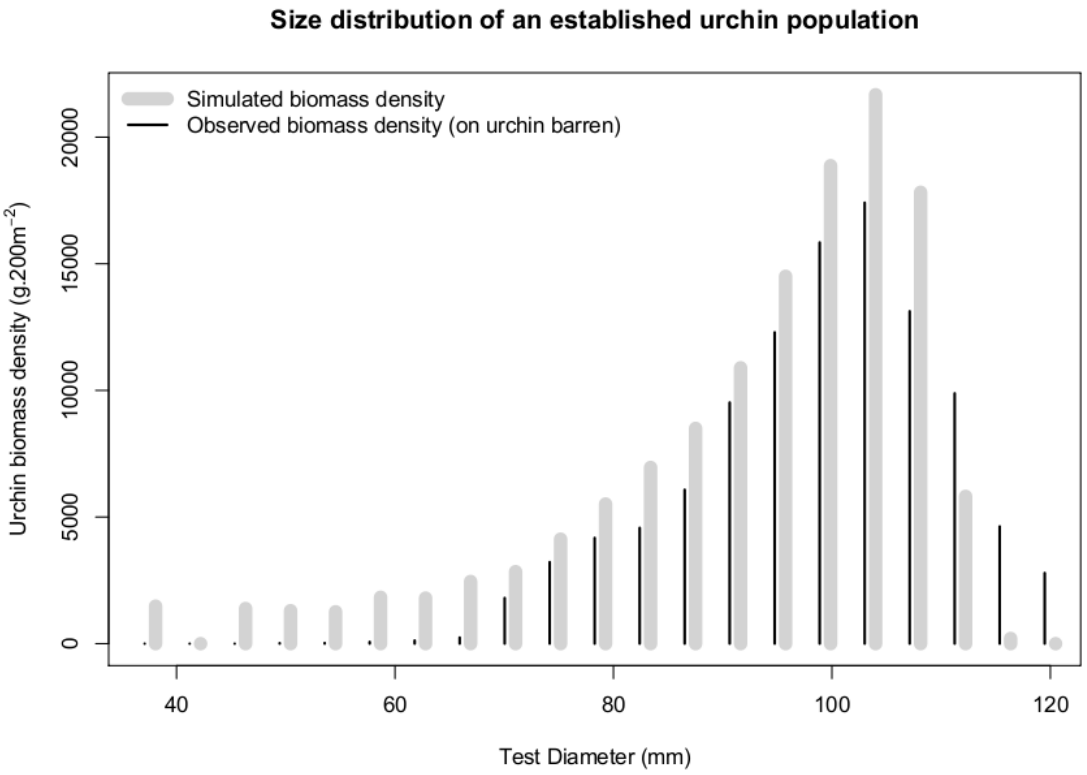


Figure A.6: Distribution of sea urchin biomass density across all modelled size classes for a fully-established urchin population (barrens state). Biomass densities (in g.200 m^{-2}) are from simulations using mean parameter estimates from Table A.2 (in grey), and from surveys at St Helens, northeastern Tasmania (in black; after Ling et al., 2009*b*).

Length-weight and allometric relationships Jaw length (JL in mm) can be converted to test diameter (TD in mm) as follows: $TD = 4.12 \times JL$ (Ling et al., 2009*b*).

The following length-weight relationship relates urchin biomass (B) in g to test diameter (TD) in mm: $B = \alpha \times TD^{\beta}$ with $\alpha = 0.00267$ ($\pm$ 0.00042 standard deviation) and $\beta = 2.534$ ($\pm$ 0.034 standard deviation) (data from Ling et al., 2009*b*).

Rock lobster size-structured dynamics

Variability of rock lobster annual recruitment on the East coast of Tasmania Lobster recruitment variability is assumed to follow a lognormal stochastic function (M. Haddon, pers. comm.; see Eq.A.4). Estimates of lobster recruitment are available from puerulus collectors on the east and southeast coast of Tasmania (Fig.A.7a and b) and from the southern rock lobster stock assessment model for the central east coast of Tasmania (Fig.A.7c). A lognormal stochastic function with standard deviation σ_{RL} of 0.6 (mean of the different estimates from Table A.3) defines inter-annual variability in lobster recruitment.

Table A.3: Estimates of the standard deviation of the lognormal distribution describing lobster recruitment inter-annual variability. Assuming a standard deviation of 0.593 coefficients for lobster stochastic recruitment function are $\gamma_{RL} = -0.15$ and $\sigma_{RL} = 0.55$ (Eq.A.4).

Site (recruitment data)	Standard Deviation
Bicheno puerulus collectors	0.52
Southeast puerulus collectors	0.53
Stock assessment for block 2	0.73

Growth transition probability matrix Lobster individual growth (mean growth increment and standard deviation) is described by third degree polynomials in the Tasmanian southern rock lobster stock assessment model (McGarvey and Feenstra, 2001). These growth functions are sex-specific and vary seasonally and spatially for each management block. Growth transition probability matrices $\mathrm{M_{s,z,t}}$ can thus be computed for each sex s, zone z and period t of the year following Eq.A.5. We averaged these matrices to produce annual transition probability matrices for each management zone across both sexes and all 4 periods of the year (because this level of details was unnecessary in our ecological model of Tasmanian reef dynamics) as follows:

$$M_z = \sum_{s=1}^{2} \Big[\prod_{t=4}^{t=1} M_{s,z,t} \Big] \times \frac{1}{2} \tag{A.8}$$

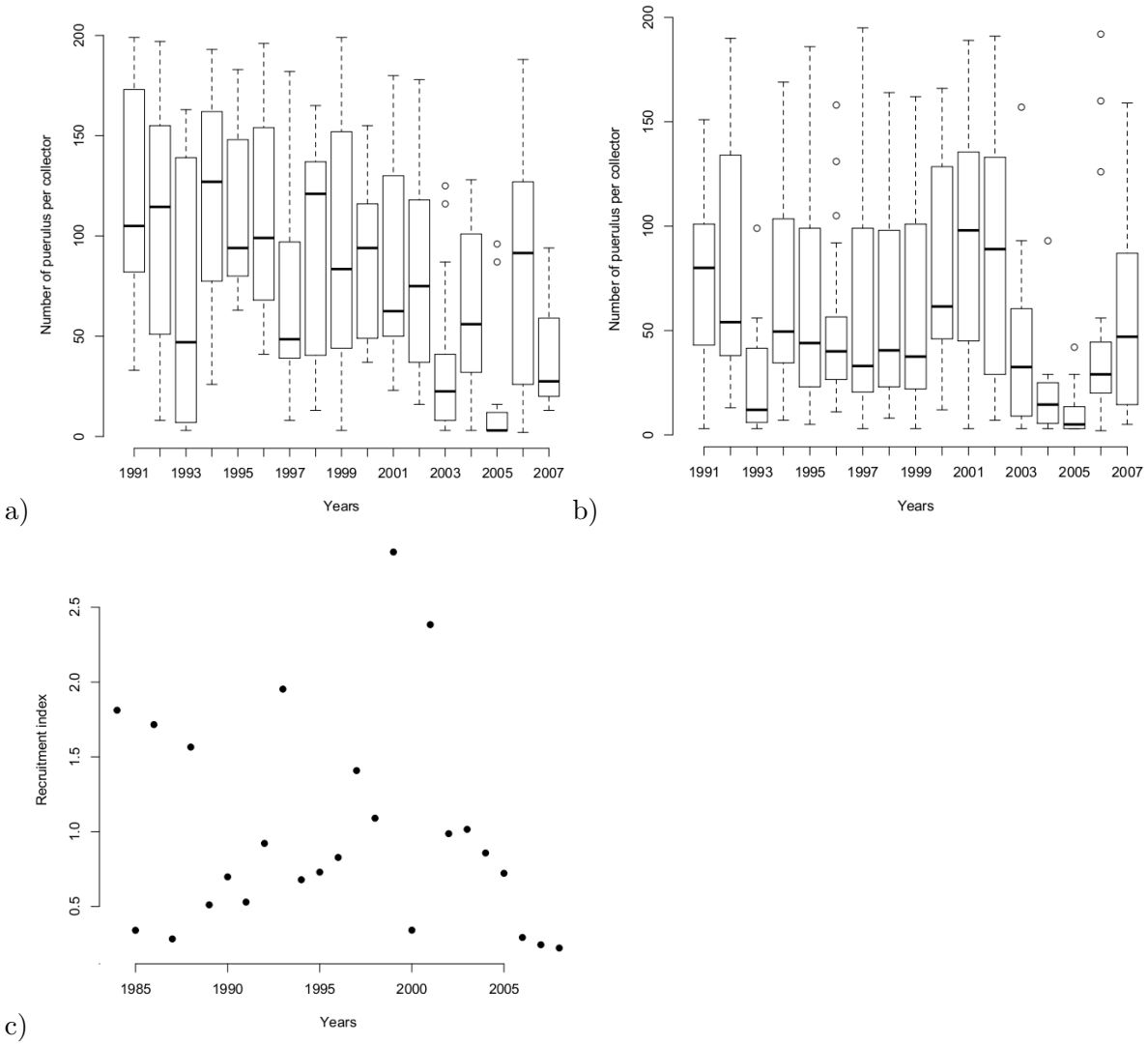


Figure A.7: Estimates of mean annual lobster recruitment on the east coast of Tasmania from puerulus collectors (Frusher, unpublished data) in a) Bicheno and b) in southeastern Tasmania from 1991 to 2007 and b) from the lobster stock assessment for management block 2, central east coast of Tasmania (Gardner, unpublished data).

For all simulation results presented in this thesis, the rock lobster size-structured model is based on the polynomial growth function for management block 2 (central east coast) in the Tasmanian rock lobster assessment model (K. Hartmann, pers. comm.; McGarvey and Feenstra, 2001).

Estimating mean recruitment and natural mortality Monte-Carlo simulations with the size-structured population dynamics model were completed with sets of mortality and mean recruitment rates covering the anticipated range of values (natural mortality

rate β_{RL} in 0.1-0.3 year^{-1}, after Frusher et al. (2008) and Frusher and Hoenig (2003); mean recruitment rate μ_{RL} in 50-2000 g.200m^{-2}.year^{-1}). The goodness of fit of the lobster size-structured population dynamics model was assessed against data of lobster population biomass recovery from underwater surveys following the establishment of the Maria Island marine reserve (see Fig. A.4; data from Barrett et al., 2009; Edgar et al., 2009). Table A.4 provides statistics of the 10% most likely sets of mean recruitment and natural mortality parameters for the lobster size-structured dynamics model. Fig. A.8 shows the distribution of rock lobster biomass density across all size classes i) in simulations based on mean estimates of natural mortality and recruitment rates and ii) as observed in Maria Island marine reserve 10-15 years after protection from fishing (2000-2007) (Barrett et al., 2009). Note that due to the low sample size in the surveys, aggregation of data in 5 mm bins of carapace length results in an uneven distribution of biomass density across all sizes (Fig. A.8). The distribution of the biomass density from simulations (in grey) is discontinuous across the small size classes because of the stochasticity of annual recruitment rate μ_{RL} to the first size class.

Table A.4: Parameter estimates for southern rock lobster size-structured population dynamics model (cf. Eq.A.3 and Eq.A.4).

	Unit	Mean	Range
Natural mortality β_{RL}	year^{-1}	**0.23**	0.20-0.26
Mean recruitment rate μ_{RL}	g.200m^{-2}.year^{-1}	**350**	200-800

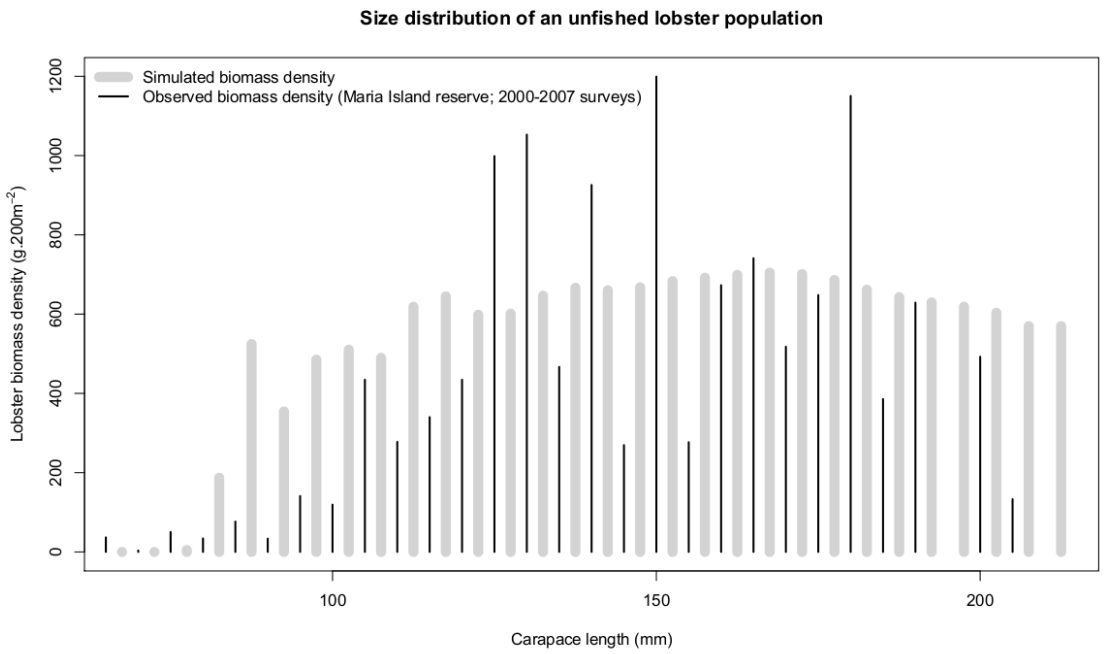


Figure A.8: Distribution of rock lobster biomass density across all modelled size classes. Biomass density (in g.200 m^{-2}) are from simulation based on mean parameter estimates from Table A.4 (in grey) and from visual surveys in Maria Island in 2000-2007 (in black; after Barrett et al., 2009).

A.2.3 Lobster dependency on the state of the seaweed bed

The rationale behind scaling lobster population dynamics by the local extent of barrens habitat relies on expert opinion and empirical evidence (e.g. Guest et al., 2009) suggesting that dense seaweed beds provide an essential habitat and source of food to rock lobster (directly and indirectly in hosting a range of small invertebrates species). Recruitment of juveniles is possibly facilitated by the presence of a seaweed canopy that provides a three-dimensional structure for the pelagic larvae to settle. Therefore, barrens formation is likely to induce a significant loss of productivity and/or recruitment for lobster population (Johnson et al., 2005; Ling, 2008).

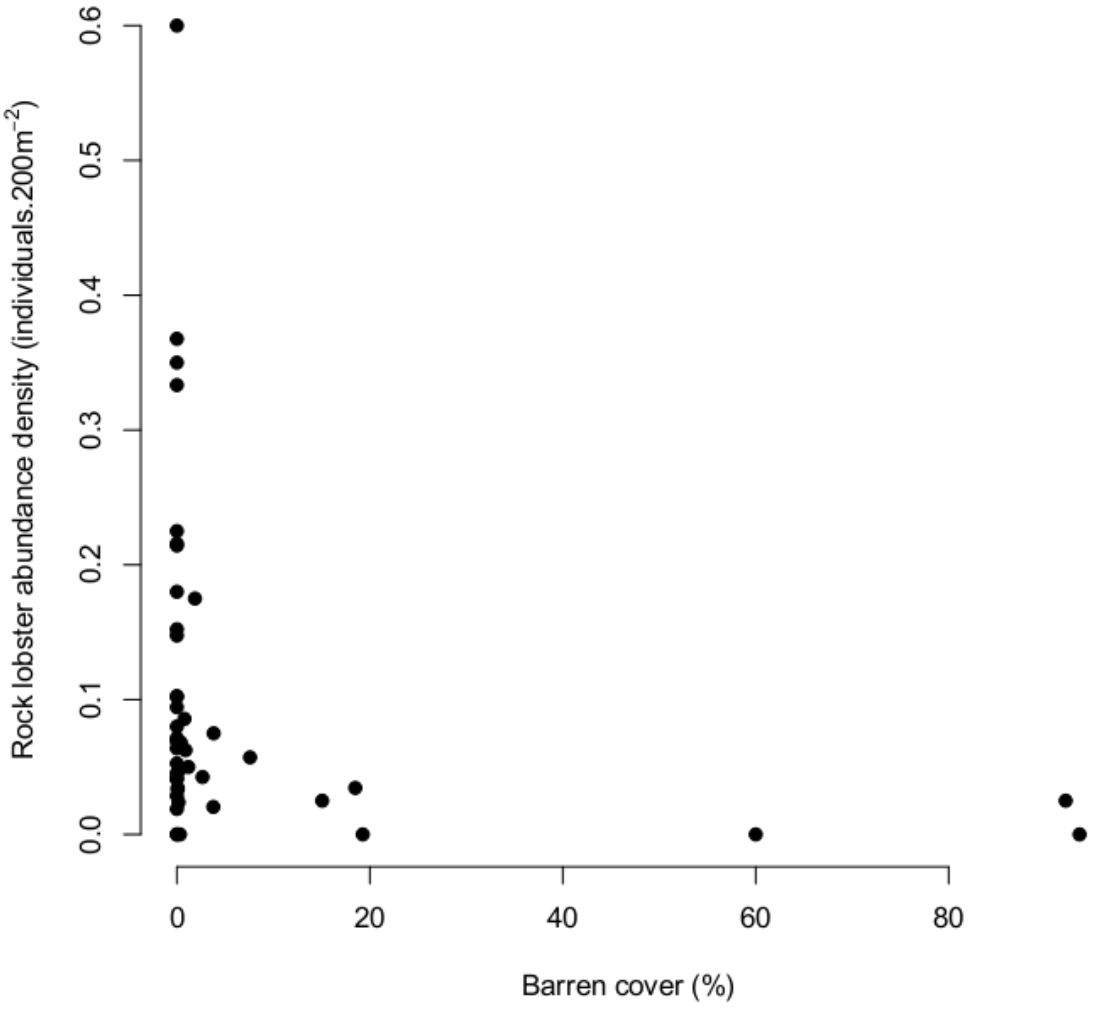


Figure A.9: Sea urchin barrens percentage cover against rock lobster density. These data from large-scale surveys of *C. rodgersii* barrens on the east coast of Tasmania are aggregated by subsite (Johnson et al., 2005).

Correlative data from large-scale survey A large-scale survey of sea urchin barrens was conducted in 2000 along the east coast of Tasmania from the Kent group (Bass Strait) to Recherche Bay (southeastern Tasmania) (Johnson et al., 2005). Sampling was hierarchically structured with 16 primary sites (13 on Tasmanian mainland; three in the Furneaux Islands group) approximately equidistant every 25-30 km along the linear coastline, which were each sub-sampled at 3 sub-sites ca. 0.3-0.5 km apart. For each sub-site, divers surveyed i) seaweed cover and composition, ii) barrens area, and densities of iii) sea urchins, iv) rock lobsters and v) abalone to 1 m on each side of four 100 m transect lines. Data were aggregated at the sub-site level (mean across all 4 transects) to quantify rock lobster population reliance on the state of the seaweed bed. The original survey data used to quantify lobster dynamics on the state of the seaweed bed is presented in Fig.A.9.

To match the scaling coefficient that defines lobster population dynamics dependency to seaweed bed in the model, barrens cover was translated into seaweed bed biomass density using the conversion factor presented in Fig.A.1a. Size was not reported for lobster individuals, so abundance density was assumed to be linearly related to biomass density (unit of model state variable). To obtain an estimate between 0 and 1, both lobster and seaweed bed densities were expressed as relative densities standardised by the maximum observed density.

The relationship between extent of barrens (we used seaweed cover as biomass density for consistency with explicit model groups) and lobster abundance is characteristic of a factor-ceiling distribution. Therefore, analysis techniques for triangular distributions were applied to quantify the relationships between extent of barrens and lobster abundance (Thomson et al., 1996; Koenker and Park, 1996). We used the non linear quantile regression function *nlrq* (Koenker and Park, 1996) from R's *quantreg* package (R Development Core Team, 2010) to estimate the three parameters of a n-th power function defined as: $B_{RL} = \alpha + \beta(B_{SW})^{\gamma}$ with B_{RL} rock lobster relative density and B_{SW} seaweed bed relative biomass density.

Comparing catch data in barrens and kelp habitat An alternative and more conservative approach to scale lobster dynamics to the state of the seaweed bed relies on fisheries-independent estimates of lobster abundance (size-specific catch per unit of effort) in both kelp and barrens habitats. Large lobsters were translocated onto extensive

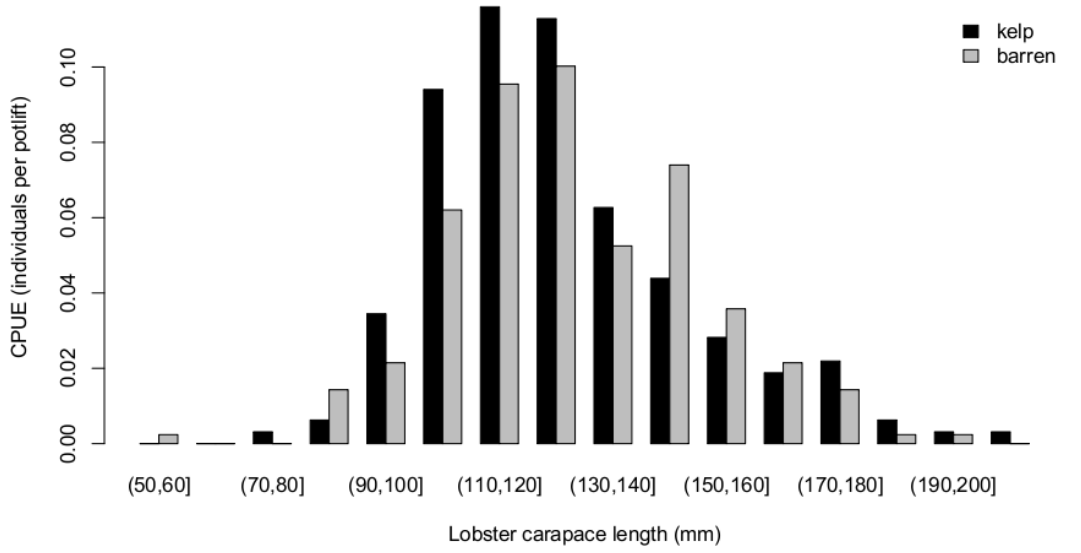
sea urchin barrens areas off the coast of Tasmania. The experimental site at Elephant Rock was closed to fishing for the past three years to gauge the efficiency of translocating deep sea lobsters (carapace length (CL) superior to 140 mm) as a management option to restore seaweed habitat from fully-established urchin barren (Johnson, unpublished data). Both translocated and resident lobster populations were sampled bi-annually using fishing traps. Note, that the extensive sea urchin barrens at Elephant Rock has adjacent kelp habitat in the shallow (depth inferior to 12 m), which is typical of extensive *C. rodgersii* barrens on the east coast of Tasmania.

Catchability estimates vary between the two habitats (barrens versus seaweed beds) with lobster being more catchable on barrens grounds (more mobile and possibly foraging more actively). Capture-mark-recapture modelling of tagged animals in the Elephant Rock experimental site provides habitat-specific estimates of catchability coefficients (as percentage of the population sampled through potting) across all size classes of lobster. Depending on the assumptions of the fitted model (independent population on barrens and seaweed bed habitat; single population with individuals migrating between the two habitats), the estimated percentage of the population sampled by pot-fishing vary between 1.4 (+/- 1.7) - 9.9 (+/- 10.0) % in the kelp bed or 7.5 (+/- 2.3) - 11.6 (+/- 2.8) % (+/- standard error) on barrens habitat. Ratio in catchability between the two habitats (kelp bed versus barrens ground) estimates to be 0.18 to 0.85. Similar work on habitat (barrens versus kelp bed)-specific catchability for American rock lobster in Nova Scotia suggests a ratio of 0.766 of catchability in kelp bed relative to barrens habitat (Miller, 1989) .

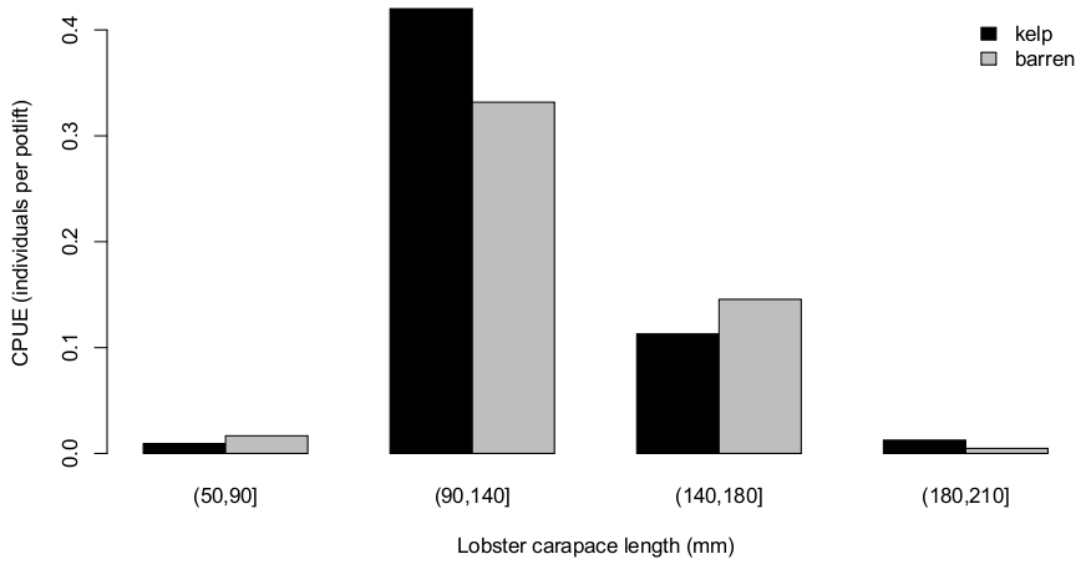
Figure A.10 shows the size-structured distribution of catch per unit of effort in both habitats. To interpret these data in terms of effects of barrens habitat on lobster population abundance and dynamics, we excluded the lower (carapace length < 90 mm) and upper (carapace length > 180 mm) tails of the size distribution because of the low sample size (less than 0.02 individuals per potlift). Additionally, only the abundance of smaller size classes of lobster (carapace length inferior to 140mm) is lower on barrens ground than in adjacent kelp beds (see Fig. A.10). The abundance of large lobsters (carapace length $>$ 140 mm) looks similar in both habitats. This suggests that large lobsters do equally well in both habitats. Therefore, only lobster recruitment is scaled by the state of the seaweed bed in the model.

To account for the effects of clustering the catch data across individual sizes, we used

different levels of aggregation (size classes of 10 or 20 mm, or 4 size classes defined as: 50 - 90 mm; 90 - 140 mm; 140 - 180 mm; 180 - 210 mm; cf. Table A.5) to compare the abundance of lobster on barrens ground compared to adjacent seaweed beds. The abundance of small size classes of lobster (carapace length between 90 - 140 mm) on barrens is 0.76 (+/- 0.13 standard deviation; $\beta_{RL,SW}$ parameter in TRITON) times the abundance of similar sizes in the adjacent seaweed beds.



a)



b)

Figure A.10: Size-structured catch per unit of effort (individuals per potlift) in the Elephant Rock experimental area following protection from fishing in both seaweed (black) and barrens (grey) habitats.

Table A.5: Size-Structured catch per unit of effort (CPUE; the unit is individuals per potlift) in the St Helens experimental site following protection from fishing for resident lobsters onlye (translocated animals are excluded). We use different levels of aggregation across size classes for both seaweed bed and sea urchin barrens habitat. The ratio of $CPUE_{barren}$ to $CPUE_{kelp}$ provides a proxy for the effects of extent of barrens on lobster abundance. The ratios of CPUE account for differences in catchability in the two habitats; indeed, catchability estimates from Elephant Rock suggest that 9.9 % of the resident population was sampled through potting in the kelp bed against 11.6% on barrens ground.

	Lobster CL (mm)			
	50-90	90-140	140-180	180-210
$CPUE_{kelp}$	0.01	0.42	0.113	0.01
$CPUE_{barren}$	0.02	0.33	0.146	0.004
$CPUE_{barren}/CPUE_{kelp}$ (corrected for catchability)	1.52	0.67	1.10	0.32

Lobster CL	Width of size classes	Mean of $CPUE_{barren}/CPUE_{kelp}$ (+/- Standard deviation)
	Raw catch data	
90-130 mm	20 mm	0.753 (+/- 0.145)
130-190 mm	20 mm	0.999 (+/- 0.353)
90-140 mm	10 mm	0.766 (+/- 0.117)
40-180 mm	10 mm	1.187 (+/- 0.423)
	Catch data corrected for habitat-specific catchability	
90-130 mm	20 mm	0.64 (+/- 0.12)
130-190 mm	20 mm	0.85 (+/- 0.30)
90-140 mm	10 mm	0.65 (+/- 0.10)
40-180 mm	10 mm	1.01 (+/- 0.36)

A.3 Trophic interactions

A.3.1 Sea urchin grazing on seaweed

Data The estimate of *Centrostephanus rodgersii* grazing rate on seaweed was derived from a feeding experiment completed *in situ* in New-South-Wales (Hill et al., 2003). For 4-5 days, individual sea urchins were fed a range of algal species similar to those encountered on Tasmanian rocky-reefs.

Parameter estimate Overall, daily consumption of seaweed per individual sea urchin (of test diameter between 80 and 90 mm) was 3.23 g (Hill et al., 2003). Using the length weight relationship for *C. rodgersii* in Tasmania ($B = 0.00267 \times TD^{2.53}$ with B individual biomass in g; TD test diameter ranging from 75 to 95 mm to conservatively envelop uncertainty), the biomass-based sea urchin grazing rate on seaweed, $\beta_{SW,CR}$, was 5.94 ($\pm$ 1.10 standard deviation) year^{-1} (i.e. g of seaweed. g of urchin^{-1} .year^{-1}).

Comparison with other estimates of grazing rates In a model of urchin feeding fronts in Nova Scotia, Canada (Lauzon-Guay et al., 2009), grazing rate is a constant and takes values of either zero, or a positive constant once sufficient individuals gather to form a feeding front. The assumption that sea urchins have to aggregate to a threshold density for efficient grazing does not apply to *C. rodgersii* grazing on Tasmania rocky-reefs, as *C. rodgersii* does not form feeding aggregations. Destructive grazing of seaweed beds appears to occur as the sum of independent grazing by individual urchins.

Our estimate of urchin grazing rate from Hill et al. (2003) is of the same order as other studies of temperate sea urchin species, even though the mean value is almost twice half that on feeding fronts in Nova Scotia (rate of 10.9 g of seaweed. g of urchin^{-1} .year^{-1}) (Lauzon-Guay et al., 2009). This reflects a difference in the per capita intensity of urchin grazing in Tasmania compared to destructive grazing in feeding fronts consuming northwestern Atlantic seaweed beds.

Functional response The effects of grazing rate formulation can have significant effects on the behaviour of marine ecosystem models (Fulton et al., 2003*b*). Experiments have identified consequences of grazing by temperate sea urchin to be density-dependent (Hill

et al., 2003; Wright et al., 2005). In models of plant-grazer dynamics, a range of density-dependent functional responses have been used to represent the grazing terms, including both Holling type III (e.g. Scheffer et al., 2008) and Holling type II (e.g. Sommer, 1999) functional responses. However, quantitative observations or experimental evidence are lacking to guide the choice of the most appropriate functional response for grazing by *C. rodgersii* in Tasmania. In particular, knowledge of the effects of both seaweed and urchin biomass density on *C. rodgersii* grazing rate is lacking. However, our sensitivity analysis indicates that the influence of grazing rate and its formulation on model dynamics is minor relative to other parameters such as lobster predation rates on urchin, recruitment rates or fishing mortality.

For the purpose of simplicity and in the absence of supporting data, the intensity of urchin grazing in TRITON is simply assumed to be linearly proportional to sea urchin biomass density. The use of this simple representation of urchin grazing on seaweed is justified because our model focuses on the top-down effect of urchin grazing as a destructive process depleting Tasmanian seaweed beds. The actual intake of food through grazing does not affect sea urchin population dynamics in the model since sea urchin populations are able to feed on drift materials and sustain high biomass density on barrens in the absence of standing macroalgae (Ling and Johnson, 2009).

Limitations and future improvements The contribution of storm events to the depletion of kelp beds is not explicitly addressed in our model. It is possible however that storm events may significantly facilitate barrens formation with swell action physically removing large macroalgal individuals (Reed et al., 2011), which supply propagules to the environment as well as shelter for juvenile plants. However, this phenomenon is currently little documented and quantified around Tasmania.

Kelp blades can have a whip lashing effect on sea urchin in exposed reefs (Clemente and Hernandez, 2008). However, *C. rodgersii* has been observed to climb up individual plants, so that adult macroalgae do not attain a size refuge. *C. rodgersii* also graze on the holdfast binding the plant to the reef, which can cause loss of biomass. In term of long-term biomass loss, the effects of urchin grazing on adult plants may well be as important as on juvenile ones, although further observations are required to represent the effects of urchin grazing on individual macroalgae with finer details. In summary, we assume that the whole pool

of seaweed is grazed upon by sea urchins, as size-specific availability of seaweed to urchins is not currently quantified.

A.3.2 Lobster predation on sea urchins

Lobster predation rates on sea urchins

Data from *in situ* predation experiments Survivability estimates of sea urchins were available from a tagging experiment within and outside two marine reserves on the East coast of Tasmania, where rock lobsters are the only effective predator of *C. rodgersii* (Ling et al., 2009*a*). Urchin biomass density was relatively even across all sites (48 tagged urchins were released in each site). Despite some contrasts in lobster density between sites (especially between fished and unfished areas), fitting predator-dependent functional responses (Skalski and Gilliam, 2001; Kratina et al., 2009) of sea urchin mortality due to lobster predation was not meaningful . Note that 1) the density of sea urchins is very low in this manipulative experiment (about 20 times sparser than observed density in barrens habitat), and that 2) sea urchin survival in fished areas, where predation-capable lobster abundance is very low, does not provide information about lobster predation but rather about other sources of mortality. Some estimates of lobster predation on urchin can be derived from this data (Table A.7) but it is essential to keep in mind that the density of urchin was very low in this experiment.

Data from DNA analysis of lobster faeces at two experimental sites Data from DNA analysis of prey items in lobster faecal pellets provided an alternative source of information about the frequency of lobster predation events on urchin (Redd et al., 2008). Samples of lobster faecal pellets were collected from two experimental sites (Redd, unpublished data) at Elephant Rock near St Helens (594 samples) and North Bay on the Forestier Peninsula (692 samples), where extensive and incipient sea urchin barrens occur respectively.

However, these data require cautious interpretation as rock lobster faeces can be positive to DNA of the sea urchin through scavenging of sea urchin remains, or ingestion of *C. rodgersii* faecal pellets from the sediment. Thus, presence of urchin DNA in the sediment constitutes a possible source of false positives.

Potential false positives in the DNA signal was accounted for in several ways.

(i) Weak positive signals are excluded as likely artefacts by using a threshold number of polymerase chain reaction (PCR) cycles (Kevin Redd, pers. comm.). A threshold of 40 cycles was chosen to exclude these weak positive signals. Comparison of predation estimates based upon DNA analysis against estimates calculated from the observed decline in urchin density at the North Bay experimental site supports the choice of this threshold.

(ii) To minimise the risk of false positives due to scavenging activity on urchin decaying carcasses, we exclusively considered DNA information for large lobster individuals capable of preying on any size of *C. rodgersii* individuals (Carapace length >= 140 mm). On average in recorded encounters of lobsters and sea urchins in the field, S.D. Ling observed 5 scavenging events for 4 predation events for small size classes of lobster, while larger size classes (carapace length >= 140 mm) did not demonstrate scavenging behaviour (data from video monitoring of predation events in Maria Island reserve; see Ling et al. (2009*a*)).

All these filters for false positive were applied to faecal pellets positive to *C. rodgersii* DNA for large lobster individuals. Thus, despite the potential for false positives, the DNA-based estimates of predation presented here (see Table A.7) are conservative.

DNA from *C. rodgersii* is detectable in rock lobster faecal samples within seven hours and up to 60 hours after ingestion (Redd et al., 2008). The proportion of lobsters feeding on the urchin (30.4 - 50.2 % of large lobster individuals eat a sea urchin every 60 hours) indicates that a large rock lobster eats 44 - 73 urchins per year. This corresponds to an overall biomass-based estimate of lobster predation rate on *C. rodgersii* of 7.5 (+/- 2.6; standard deviation) year^{-1} (i.e. g of urchin/ g of lobster/ year) across all DNA samples. Please refer to Table A.7 for site-specific estimates of predation from DNA assays of lobster faecal pellets.

Estimates of predation rates Overall, the different estimates of lobster predation from predation experiments, DNA analysis and declines in sea urchin abundance at experimental sites with known densities of predation-capable lobsters are in agreement (i.e. of the same order with values ranging from 0.3 to 9.4 g of urchin per g of lobster per year; cf. Table A.7). For the DNA-based estimates, data are only presented for large lobster (carapace length > 140mm).

Table A.7: Estimates of lobster predation rates (g of sea urchin / g of lobster / year) on sea urchins based from different data sources. Large lobsters correspond to individuals with a carapace length >=140mm.

Data source	Mean	Std. Dev.
Tagging experiment		
All lobster	0.29	0.14
Large lobsters	0.64	0.3
DNA analysis of faecal pellets	(Large lobsters)	
Elephant Rock site	9.40	3.00
North Bay site	5.71	1.82

Functional response A range of alternative functional responses dependent on lobster and urchin biomass density (Holling type I, II or III) were fitted to urchin mortality estimates using the *nls* function of the R language for statistical computing, version 2.12 (R Development Core Team, 2010). Shape of the functional response was estimated using biomass density estimates of lobster and sea urchin across all sizes (as opposed to size-specific functional responses). The most likely functional responses were selected using both Akaike and Bayesian Information Criteria. Currently available data were not sufficient to objectively inform the most adequate functional response for lobster predation.

Therefore, the most common functional responses used to describe decapod predation were reviewed from published literature (cf. Table A.8). Dependency of predation rate on lobster density (i.e. allowing for interactions among lobsters in their access to prey as described by the Beddington-De Angelis functional response; van der Meer and Smallegange, 2009) was ignored due to low contrast in lobster density in the data. Only Holling Type I, II and III functional responses were fitted to available estimates of lobster predation rate on *C. rodgersii* (cf. Table A.7).

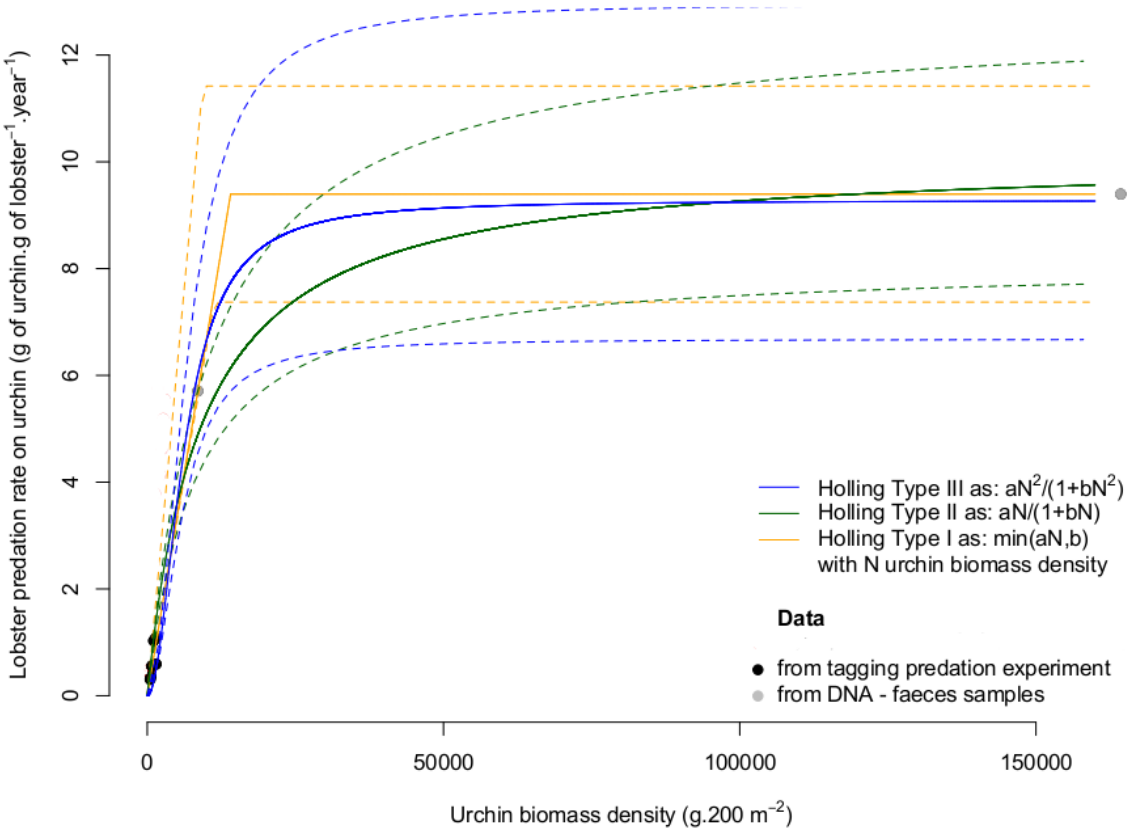


Figure A.11: Estimates of lobster predation rate on *C. rodgersii* and fitted Holling Type I (orange curve), II (green curve) and III (blue curve) functional responses to urchin density. Data from predation experiments (Ling et al., 2009*a*) in marine reserves are shown in black and data from DNA analysis of lobster faecal pellets in grey. The dotted lines represent the 50% confidence interval of the fitted functional responses.

Table A.8: Functional responses used to describe decapod predation rates. In general, a Type II functional response is well-suited if handling time is limiting at low prey density, whereas Type III responses are more appropriate if encounter probability is more likely to be limiting.

Predator	Prey	Functional response	Size-specific	Reference
American lobster *H. americanus*	Green sea urchin *S. droebachiensis*	Type III	All size	Breen, 1974; Evans and Mann, 1977 Hagen and Mann, 1992
American lobster *H. americanus*	Green sea urchin *S. droebachiensis*	Type II	Large prey only	Breen, 1974; Evans and Mann, 1977 Hagen and Mann, 1992
Shore crabs *C. maenas*	Mussel *M. edulis*	Beddington-DeAngelis (predator density-dependence)		van der Meer and Smallegange, 2009 Smallegange and van der Meer, 2010
Shore crabs *C. maenas*	Mussel *M. edulis*	Type III		Griffen and Delaney, 2007
Blue crab *C. sapidus*	Clams *M. arenaria, M. balthica*	Type III (field)		Seitz et al., 2001
Crab *C. irroratus*	Scallop *P. magellanicus*	Type II (lab.) Type III (field)	Evidence of size-structured interactions	Barbeau et al., 1998 Wong et al., 2010 Wong and Barbeau, 2006
Crabs *C. sapidus*	Clams *M. arenaria, M. balthica*	Type III (lab.) Type II (field)		Eggleston et al., 1992 Iribarne et al., 1995
Crab *C. sapidus*	Oysters *C. virginica*	Type III		Eggleston, 1990

Parameter estimates Table A.9 presents parameter estimates for the Holling type I, II and III functional responses of lobster predation on urchin.

Table A.9: Parameter estimates for the Holling Type I, II and III functional responses of lobster predation on sea urchins, $\beta_{CR,RL}$, (g of CR. g of RL^{-1}. $year^{-1}$) defined with N sea urchin biomass density (g.200m^{-2}) and where β and β' are scalars defining the shape of the functional response. Data from the in situ predation experiment (Ling et al., 2009*a*; Ling and Johnson, In press) and DNA analysis of lobster faecal pellets (Redd, unpublished data).

	Estimate	Standard error	t value	$Pr(>\|t\|)$
Holling Type I as $\beta_{CR,RL} = min(\beta\, N, \beta')$				
β	6.68×10^{-4}	2.27×10^{-5}	29.4	1.35×10^{-8}
β'	9.40	3.00		
Holling Type II as $\beta_{CR,RL} = \frac{\beta N}{1+\beta' N}$				
β	11.09×10^{-4}	1.68×10^{-4}	6.62	0.0003
β'	1.10×10^{-4}	0.20×10^{-4}	5.61	0.0008
Holling Type III as $\beta_{CR,RL} = \frac{\beta N^2}{1+\beta' N^2}$				
β	2.35×10^{-7}	0.55×10^{-7}	4.32	0.0035
β'	2.50×10^{-8}	0.60×10^{-8}	3.92	0.0058

Size-structured predation of lobster on sea urchin

Predation of rock lobsters on sea urchins is size-structured reflecting that the size of a lobsters' first pair of walking legs limits its ability to handle sea urchin (Ling et al., 2009*a*). To capture this physical threshold restricting predation, the minimum rock lobster carapace length (CL_{min}, in mm) required to predate upon sea urchin individuals of a given test diameter (TD, in mm) was defined after Ling et al. (2009*a*) as $CL_{min} = \alpha \log(TD) - \beta$ with $\alpha = 43.48$ and $\beta \in [48.91; 71.01]$ (mean of 59.96; standard deviation of 15.63).

Table A.10: Summary of all parameter estimates and confidence intervals for TRITON.

Parameter	Units	Estimate	Standard error	Confidence interval
Seaweed bed logistic growth				
α_{SW}	year^{-1}	4.43	1.65	$1.72 - 7.14$
K_{SW}	g SW.200 m^{-2}	3.4×10^5	3.6×10^4	$2.8 \times 10^5 - 4 \times 10^5$
μ_{SW}	g SW.200 m^{-2}.year^{-1}	**5000**		$2500 - 10000$
Sea urchin size-structured population growth				
β_{CR}	$year^{-1}$	**0.11**		$0.1 - 0.15$
μ_{CR}	g CR.200 m^{-2}.year^{-1}	**4100**		$2500 - 10000$
Lobster size-structured population growth				
β_{RL}	$year^{-1}$	**0.23**		$0.20 - 0.26$
μ_{RL}	g RL.200 m^{-2}.year^{-1}	**350**		$200 - 800$
Lobster dependency on the state of the seaweed bed				
$\beta_{SW,CR}$	constant	0.64	0.11	$0.46 - 0.83$

Seaweed bed logistic growth

with α, intrinsic growth rate; K, carrying capacity; μ, mean annual recruitment rate.

Sea urchin size-structured population growth
Growth transition matrix derived from Ling and Johnson, 2009.
β is the annual natural mortality; μ, the mean annual recruitment rate.

The annual stochastic recruitment function follows a binomial with a 0.4 probability of success, which is combined with a lognormal with a standard deviation σ_{CR} of 0.5.

Lobster size-structured population growth
Growth transition matrix derived from McGarvey and Feenstra, 2001.
β is the annual natural mortality; μ, the mean annual recruitment rate.

The annual stochastic recruitment function follows a lognormal with a standard deviation σ_{RL} of 0.6.

Lobster dependency on the state of the seaweed bed
Lobster recruitment is scaled by: $(1 - \beta) \times (1 - \frac{B_{SW}}{K_{SW}})$
with B_{SW}, seaweed bed biomass density; K_{SW}, seaweed bed carrying capacity.

Parameter	Units	Estimate	Standard error	Confidence interval
Urchin grazing rate				
$\beta_{SW,CR}$	g SW.g CR^{-1}.year^{-1}	5.94	1.10	4.13 – 7.75
Functional responses of lobster predation on urchin				
With B_{CR}, urchin biomass density (g. 200m^{-2}): Holling Type I as $\beta_{CR,RL} = min(\beta B_{CR}, \beta')$				
β	g RL^{-1}.year^{-1}	6.68 $\times 10^{-4}$	2.27 $\times 10^{-5}$	6.31 $\times 10^{-4}$ - 7.05 $\times 10^{-4}$
β'	g CR.g RL^{-1}.year^{-1}	9.40	3.00	4.46 - 14.33
Holling Type II as $\beta_{CR,RL} = \frac{\beta B_{CR}}{1+\beta' B_{CR}}$				
β	g RL^{-1}.year^{-1}	11.09$\times 10^{-4}$	1.68 $\times 10^{-4}$	8.34 $\times 10^{-4}$ - 13.85 $\times 10^{-4}$
β'	g CR^{-1}	1.10$\times 10^{-4}$	0.20 $\times 10^{-4}$	7.76 $\times 10^{-5}$ - 14.19 $\times 10^{-5}$
Holling Type III as $\beta_{CR,RL} = \frac{\beta (B_{CR})^2}{1+\beta' (B_{CR})^2}$				
β	g CR^{-1}.g RL^{-1}.year^{-1}	2.35 $\times 10^{-7}$	0.55 $\times 10^{-7}$	1.46 $\times 10^{-7}$ - 3.25 $\times 10^{-7}$
β'	g CR^{-1}.g CR^{-1}	2.50 $\times 10^{-8}$	0.60 $\times 10^{-8}$	1.47 $\times 10^{-8}$ - 3.60 $\times 10^{-8}$

Allometric and other size-based relationships

Length-weight relationship for the long-spined sea urchin
$B = 0.00267 \times TD^{2.534}$,
with B, urchin individual weight (g); TD, urchin test diameter (mm).

Length-weight relationship for the southern rock lobster
$B = 0.000271 \times CL^{3.135}$,
with B, lobster individual weight (g); CL, lobster carapace length (mm).

Size-Structured predation of lobster on urchin
$CL_{min} = 43.5 \times \log(TD) - \beta$, with $\beta \in [48.91 : 71.01]$
with CL, lobster carapace length (mm); TD, urchin test diameter (mm).

A.4 Implicitly accounting for other factors in the model

A.4.1 Other biotic factors: model closure

The number of functional groups explicitly described is minimal to capture the gross dynamics and focus on the effects of overgrazing of seaweed beds by the invasive long-spined sea urchin. Natural mortality accounts for other sources of mortality affecting modelled groups or species, such as predation (e.g. octopus predation on lobster) or intraspecific competition.

A.4.2 Abiotic factors: temperature, seasonality, habitat and depth

Seasonality

Several model parameters are likely to change seasonally, *viz.* growth, recruitment (spawning and settlement of pelagic larvae) and trophic interactions (catchability of southern rock lobster varies throughout the year and directly relates to lobster foraging activity). Autoregressive functions (Annan, 2001) can be implemented to capture stochasticity due to temporal variability of parameter values: $r_{t+dt} = \mu + (r_t - \mu) \times AR_{coef} + \epsilon$, with r_t, parameter value at time t; μ, the mean parameter value; $\mathrm{AR_{coef}}$ constant autoregressive parameter (lag 1 autocorrelation coefficient); ϵ a random variable taken from a Gaussian distribution with mean 0 and standard deviation s_o. The variance s_r of the resulting time series is given by the equation: ${s_r}^2 = {s_o}^2/(1 - AR_{coef})^2$ (Annan, 2001).

The current version of the model does not incorporate seasonality because implementing autoregressive stochastic functions considerably increases model complexity in terms of parameterisation, and specific information about the seasonality of the different model processes is lacking.

Temperature

Sea surface temperature essentially controls two processes in the model, urchin recruitment and lobster growth (see the section about size-structured population dynamics).

Sea urchin recruitment Sea urchin early larval stages can only develop successfully if the ambient temperature is above 12°C (Fig.A.5; Ling et al., 2008).

Discrepancies in lobster growth Lobster growth rates increases significantly with temperature on the east coast of Tasmania, and in eastern Bass Strait lobsters moult twice a year compared with a single annual moult in southern Tasmania (Punt and Kennedy, 1997). For simplicity, growth rate for the central east coast of Tasmania (i.e. region of main focus for management of sea urchin barrens in Tasmania) is used in TRITON.

Effects of habitat and depth: patchiness of reef communities

Abiotic factors that are not explicitly captured in TRITON can influence modelled processes. Model dynamics can mostly be affected by: i) depth, which correlates with declines in both swell action and light levels, which influences seaweed growth; ii) habitat structure, which can significantly influence sea urchin survival (Ling and Johnson, In press). These processes essentially affect seaweed mortality (abrasion by wave action) and growth rate (exposure to light), urchin natural mortality (exposure to predators) and the strength of lobster predation on urchin. Thus, changing the mean values of these rates through Monte-Carlo simulations with TRITON constitutes a rigorous representation of spatial patchiness in reef dynamics.

A.5 Limitations and guidance for future research

Building an ecological model provides a good opportunity to synthesise the current state of knowledge about the dynamics of a given ecosystem. Emphasising the limitations of the model due to lack of information about ecosystem processes is important to both i) recognise limitations and sources of uncertainty in model predictions, and ii) prioritise future research in addressing knowledge gaps. Limitations in current understanding of Tasmanian rocky-reef community dynamics are outlined following. Some of the data available could not be fully-exploited because the experimental context (e.g. spatial scales) was not always clearly reported, which highlights the value of sharing and reporting data from field experiments and observations in a transparent format for future re-uses.

A.5.1 Seaweed bed dynamics

Our definition of seaweed bed dynamics is based upon a single experiment, where recovery of seaweed communities from a barrens state was monitored off the coast of Bicheno, eastern Tasmania. Inclusion of additional experiments across different sites with different features in terms of depth, habitat, latitude and temperature would allow refinements of the current estimates. Additionally, it would be useful to represent guilds of seaweeds rather than represent them as a single variable.

Conversion from percentage cover to wet weight Most experiments and observations report seaweed cover in percentage cover, and only few measurements of both percentage cover and standing biomass were available to define a conversion factor from percentage cover to biomass.

Effects of depth Studies (e.g. Kirkman (1989) in Western Australia) have investigated the effect of depth on seaweed bed productivity, but this information was not readily included into TRITON, which does not account for depth explicitly.

A.5.2 Dependency of lobster dynamics to the state of the seaweed bed

Current data from large-scale surveys of the extent of sea urchin barrens and lobster density provides the best information to quantify the effect of barrens habitat on lobster

population dynamics (recruitment rates in particular). However, the effect of barrens on the lobster life cycle (e.g. puerulus settlement or growth) may not be responsible for these large-scale patterns (Johnson et al., 2005). Other causal mechanisms such as local depletion of lobster abundance by fishing could drive correlations observed between lobster abundance and seaweed bed cover.

A.5.3 Urchin grazing rate on seaweed

In the model, all of the seaweed standing biomass is assumed to be available to sea urchins for consumption. A more realistic representation of these processes would require further studies on the effects of urchin grazing on seaweed holdfasts and the temporal dynamics of individual macroalgal abrasion of the substratum following sea urchin grazing. Additionally, no data are currently available to quantify density dependence of the grazing rate on either the seaweed bed cover or sea urchin density.

A.5.4 Predation rate

While predation estimates from DNA analysis may be skewed by false positive signals (under current investigation), *in situ* predation experiments were completed at very low urchin density (an order of magnitude sparser than on urchin barren). Thus, our current estimate of predation rate could be refined based on further analysis of DNA sample and further field experiments with higher densities of sea urchin. More sophisticated functional responses (e.g. Beddington-De Angelis accounting for dependency to lobster biomass density) would also require further manipulative experiments.

References

Andrew, N. 1993. Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. Ecology 74:pp. 292–302.

Andrew, N. L., Agatsuma, Y., Ballesteros, E., Bazhin, A. G., Creaser, E. P., Barnes, D. K. A., Botsford, L. W., Bradbury, A., Campbell, A., Dixon, J. D., Einarsson, S., Gerring, P. K., Hebert, K., Hunter, M., Hur, S. B., Johnson, C. R., Juinio-Menez, M. A., Kalvass, P., Miller, R. J., Moreno, C. A., Palleiro, J. S., Rivas, D., Robinson, S. M. L., Schroeter, S. C., Steneck, R. S., Vadas, R. L., Woodby, D. A., and Xiaoqi, Z. 2002. Status and management of world sea urchin fisheries. Oceanography and Marine Biology, Vol 40 40:343–425.

Andrew, N. L. and O'Neill, A. L. 2000. Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. Marine and Freshwater Research 51:255–263.

Andrew, N. L. and Underwood, A. J. 1989. Patterns of abundance of the sea urchin *Centrostephanus rodgersii* (Agassiz) on the central coast of New-South-Wales, Australia. Journal of Experimental Marine Biology and Ecology 131:61–80.

Annan, J. D. 2001. Modelling under uncertainly: Monte carlo methods for temporally varying parameters. Ecological Modelling 136:297–302.

Banks, S. C., Ling, S. D., Johnson, C. R., Piggott, M. P., Williamson, J. E., and Beheregaray, L. B. 2010. Genetic structure of a recent climate change-driven range extension. Molecular Ecology 19:2011–2024.

Banks, S. C., Piggott, M. P., Williamson, J. E., and Beheregaray, L. B. 2007. Microsatellite DNA markers for analysis of population structure in the sea urchin *Centrostephanus rodgersii*. Molecular Ecology Notes 7:321–323.

Barbeau, M. A., Scheibling, R. E., and Hatcher, B. G. 1998. Behavioural responses of predatory crabs and sea stars to varying density of juvenile sea scallops. Aquaculture 169:87–98.

Barrett, N., Buxton, C., and Gardner, C. 2009. Rock lobster movement patterns and population structure within a Tasmanian marine protected area inform fishery and conservation management. Marine and Freshwater Research 60:417–425.

Barrett, N. S., Edgar, G. J., Buxton, C. D., and Haddon, M. 2007. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. Journal of Experimental Marine Biology and Ecology 345:141–157.

Beisner, B. E., Haydon, D. T., and Cuddington, K. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382.

Boschetti, F., Grigg, N. J., and Enting, I. 2011. Modelling = conditional prediction. Ecological Complexity 8:86–91.

Breen, P., 1974. Relations among lobsters, sea urchins and kelp in Nova Scotia. Ph.D. thesis, Dalhousie University.

Briske, D. D., Washington-Allen, R. A., Johnson, C. R., Lockwood, J. A., Lockwood, D. R., Stringham, T. K., and Shugart, H. H. 2010. Catastrophic thresholds: A synthesis of concepts, perspectives, and applications. Ecology and Society 15:12.

Bruce, B., Griffin, D., and Bradford, R., 2007. Larval transport and recruitment processes of southern rock lobster. FRDC report Project No. 2002/007. Technical report, CSIRO.

Cariboni, J., Gatelli, D., Liska, R., and Saltelli, A. 2007. The role of sensitivity analysis in ecological modelling. Ecological Modelling 203:167–182.

Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W. A., Cline, T., Coloso, J., Hodgson, J. R., Kitchell, J. F., Seekell, D. A., Smith, L., and Weidel, B. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. Science 332:1079–1082.

Chapman, A. R. O. and Johnson, C. R. 1990. Disturbance and organization of macroalgal assemblages in the northwest Atlantic. Hydrobiologia 192:77–121.

Christensen, V. and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172:109–139.

Cinquin, O. and Demongeot, J. 2002. Positive and negative feedback: Striking a balance between necessary antagonists. Journal of Theoretical Biology 216:229–241.

Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W. V., Rose, K. A., Sala,

O., Schlesinger, W. H., Wall, D. H., and Wear, D. 2001. Ecological forecasts: An emerging imperative. Science 293:657–660.

Clemente, S. and Hernandez, J. C. 2008. Influence of wave exposure and habitat complexity in determining spatial variation of the sea urchin *Diadema aff. antillarum* (echinoidea: Diadematidae) populations and macroalgal cover (Canary Islands - Eastern Atlantic Ocean). Revista De Biologia Tropical 56:229–254.

Coleman, M. A., Roughan, M., Macdonald, H. S., Connell, S. D., Gillanders, B. M., Kelaher, B. P., and Steinberg, P. D. 2011. Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. Journal of Ecology 99:1026–1032.

Condie, S. A., Waring, J., Mansbridge, J. V., and Cahill, M. L. 2005. Marine connectivity patterns around the Australian continent. Environmental Modelling & Software 20:1149–1157.

Cury, P. M., Shannon, L. J., Roux, J. P., Daskalov, G. M., Jarre, A., Moloney, C. L., and Pauly, D. 2005. Trophodynamic indicators for an ecosystem approach to fisheries. Ices Journal of Marine Science 62:430–442.

Cury, P. M., Shin, Y. J., Planque, B., Durant, J. M., Fromentin, J. M., Kramer-Schadt, S., Stenseth, N. C., Travers, M., and Grimm, V. 2008. Ecosystem oceanography for global change in fisheries. Trends in Ecology & Evolution 23:338–346.

Dambacher, J. M., Gaughan, D. J., Rochet, M. J., Rossignol, P. A., and Trenkel, V. M. 2009. Qualitative modelling and indicators of exploited ecosystems. Fish and Fisheries 10:305–322.

Dambacher, J. M., Levins, R., and Rossignol, P. A. 2005. Life expectancy change in perturbed communities: Derivation and qualitative analysis. Mathematical Biosciences 197:1–14.

Dambacher, J. M., Li, H. W., and Rossignol, P. A. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology 83:1372–1385.

Dambacher, J. M., Li, H. W., and Rossignol, P. A. 2003. Qualitative predictions in model ecosystems. Ecological Modelling 161:79–93.

Dambacher, J. M. and Ramos-Jiliberto, R. 2007. Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. Quarterly Review of Biology 82:227–250.

de Young, B., Barange, M., Beaugrand, G., Harris, R., Perry, R. I., Scheffer, M., and Werner, F. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends in Ecology & Evolution 23:402–409.

de Young, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., and Shannon, L. 2004. Detecting regime shifts in the ocean: data considerations. Progress in Oceanography 60:143–164.

Deng, B. 2008. The time invariance principle, the absence of ecological chaos, and a fundamental pitfall of discrete modeling. Ecological Modelling 215:287–292.

Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., Monson, D. H., Tinker, M. T., Williams, T. M., Wootton, J. T., Carroll, I., Emmerson, M., Micheli, F., and Novak, M. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology 89:952–961.

Donahue, M. J., Desharnais, R. A., Robles, C. D., and Arriola, P. 2011. Mussel bed boundaries as dynamic equilibria: Thresholds, phase shifts, and alternative states. American Naturalist 178:612–625.

Duboz, R., Versmisse, D., Travers, M., Ramat, E., and Shin, Y. J. 2010. Application of an evolutionary algorithm to the inverse parameter estimation of an individual-based model. Ecological Modelling 221:840–849.

Edgar, G. J., Barrett, N. S., and Stuart-Smith, R. D. 2009. Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. Ecological Applications 19:1967–1974.

Eggleston, D. B. 1990. Functional responses of blue crabs *Callinectes sapidus* (Rathbun) feeding on juvenile oysters *Crassostrea virginica* (Gmelin) : Effects of predator, sex and size, and prey sizeh. Journal of Experimental Marine Biology and Ecology 143:73–90.

Eggleston, D. B., Lipcius, R. N., and Hines, A. H. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Marine Ecology-Progress Series 85:55–68.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soule, M. E., Virtanen, R., and Wardle, D. A. 2011. Trophic downgrading of planet earth. Science 333:301–306. Times Cited: 0.

Evans, P. D. and Mann, K. H. 1977. Selection of prey by American lobster (*Homarus americanus*) when offered a choice between sea urchins and crabs. Journal of the Fisheries Research Board of Canada 34:2203–2207.

Firn, J., House, A. P. N., and Buckley, Y. M. 2010. Alternative states models provide an effective framework for invasive species control and restoration of native communities. Journal of Applied Ecology 47:96–105.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 35:557–581.

Francis, R. and Shotton, R. 1997. "risk" in fisheries management: a review. Canadian Journal of Fisheries and Aquatic Sciences 54:1699–1715.

Frusher, S. D., Burch, P., MacKinnon, C., and Wotherspoon, S., 2008. Developing tagging models and validating key assumptions for estimating crucial fishery assessment parameters in the Tasmanian rock lobster fishery. Technical Report 2003/051, University of Tasmania.

Frusher, S. D. and Hoenig, J. M. 2003. Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models. Fisheries Research 65:379–390.

Fulton, E. A., Smith, A. D. M., and Johnson, C. R. 2003*a*. Effect of complexity on marine ecosystem models. Marine Ecology-Progress Series 253:1–16.

Fulton, E. A., Smith, A. D. M., and Johnson, C. R. 2003*b*. Mortality and predation in ecosystem models: is it important how these are expressed? Ecological Modelling 169:157–178.

Fung, T., Seymour, R. M., and Johnson, C. R. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92:967–982.

Gardner, C. and Van Putten, E. I. 2008. Biological modeling of translocation as a management tool for a rock lobster fishery. Reviews in Fisheries Science 16:81–90.

Genkai-Kato, M. 2007. Regime shifts: catastrophic responses of ecosystems to human impacts. Ecological Research 22:214–219.

Griffen, B. D. and Delaney, D. G. 2007. Species invasion shifts the importance of predator dependence. Ecology 88:3012–3021.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H. H., Weiner, J., Wiegand, T., and DeAngelis, D. L. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. Science 310:987–991.

Guest, M. A., Frusher, S. D., Nichols, P. D., Johnson, C. R., and Wheatley, K. E. 2009. Trophic effects of fishing southern rock lobster *Jasus edwardsii* shown by combined fatty acid and stable isotope analyses. Marine Ecology-Progress Series 388:169–184.

Guest, M. A., Nichols, P. D., Frusher, S. D., and Hirst, A. J. 2008. Evidence of abalone (*Haliotis rubra*) diet from combined fatty acid and stable isotope analyses. Marine Biology 153:579–588.

Hagen, N. T. and Mann, K. H. 1992. Functional response of the predators American lobster *Homarus americanus* (Milne Edwards) and atlantic wolffish *Anarhichas lupus* (L.) to increasing numbers of the green sea urchin *Strongylocentrotus droebachiensis* (Muller). Journal of Experimental Marine Biology and Ecology 159:89–112.

Hall, S. J. and Mainprize, B. 2004. Towards ecosystem-based fisheries management. Fish and Fisheries 5:1–20.

Hastings, A. and Wysham, D. B. 2010. Regime shifts in ecological systems can occur with no warning. Ecology Letters 13:464–472.

Hernandez, J. C., Clemente, S., Girard, D., Perez-Ruzafa, A., and Brito, A. 2010. Effect of temperature on settlement and postsettlement survival in a barrens-forming sea urchin. Marine Ecology-Progress Series 413:69–80.

Hill, N. A., Blount, C., Poore, A. G. B., Worthington, D., and Steinberg, P. D. 2003. Grazing effects of the sea urchin *Centrostephanus rodgersii* in two contrasting rocky reef habitats: effects of urchin density and its implications for the fishery. Marine and Freshwater Research 54:691–700.

Holbrook, N. J. and Bindoff, N. L. 1997. Interannual and decadal temperature variability in the southwest Pacific Ocean between 1955 and 1988. Journal of Climate 10:1035–1049.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomology Society of Canada page 86.

Hosack, G. R., Hayes, K. R., and Dambacher, J. M. 2008. Assessing model structure uncertainty through an analysis of system feedback and bayesian networks. Ecological Applications 18:1070–1082.

Hosack, G. R., Li, H. W., and Rossignol, P. A. 2009. Sensitivity of system stability to model structure. Ecological Modelling 220:1054–1062.

Huggett, M. J., King, C. K., Williamson, J. E., and Steinberg, P. D. 2005. Larval development and metamorphosis of the Australian diadematid sea urchin *Centrostephanus rodgersii*. Invertebrate Reproduction & Development 47:197–204.

Iribarne, O., Armstrong, D., and Fernandez, M. 1995. Environmental impact of intertidal juvenile dungeness crab habitat enhancement: effects on bivalves and crab foraging rate. Journal of Experimental Marine Biology and Ecology 192:173–194.

Irving, A. D. and Connell, S. D. 2006. Physical disturbance by kelp abrades erect algae from the understorey. Marine Ecology-Progress Series 324:127–137.

Irving, A. D., Connell, S. D., and Elsdon, T. S. 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. Journal of Experimental Marine Biology and Ecology 310:1–12.

Johnson, C., Ling, S. D., Ross, J., Shepherd, S., and Miller, K., 2005. Establishment of the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania: first assesment of potential threats to fisheries. Technical report, Tasmanian Aquaculture & Fisheries Institute.

Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., Frusher, S. D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K. L., Holbrook, N. J., Hosie, G. W., Last, P. R., Ling, S. D., Melbourne-Thomas, J., Miller, K., Pecl, G. T., Richardson, A. J., Ridgway, K. R., Rintoul, S. R., Ritz, D. A., Ross, D. J., Sanderson, J. C., Shepherd, S. A., Slotvvinski, A., Swadling, K. M., and Taw, N. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community

dynamics in eastern tasmania. Journal of Experimental Marine Biology and Ecology 400:17–32.

Johnson, C. R. and Mann, K. H. 1988. Diversity, patterns of adaptation, and stability of Nova-Scotia kelp beds. Ecological Monographs 58:129–154.

Kirkman, H. 1984. Standing stock and production of *Ecklonia radiata* (C. Agardh). Journal of Experimental Marine Biology and Ecology 76:119–130.

Kirkman, H. 1989. Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artificial shading off Perth, Western Australia. Australian Journal of Marine and Freshwater Research 40:169–177.

Klepper, O. 1997. Multivariate aspects of model uncertainty analysis: Tools for sensitivity analysis and calibration. Ecological Modelling 101:1–13.

Koenker, R. and Park, B. J. 1996. An interior point algorithm for nonlinear quantile regression. Journal of Econometrics 71:265–283.

Kot, M., 2001. Elements of mathematical ecology. Cambridge University Press.

Kratina, P., Vos, M., Bateman, A., and Anholt, B. R. 2009. Functional responses modified by predator density. Oecologia 159:425–433.

Laskey, K. B. 1996. Model uncertainty: Theory and practical implications. Ieee Transactions on Systems Man and Cybernetics Part a-Systems and Humans 26:340–348.

Lauzon-Guay, J. S., Scheibling, R. E., and Barbeau, M. A. 2009. Modelling phase shifts in a rocky subtidal ecosystem. Marine Ecology-Progress Series 375:25–39.

Lawrence, D., D'Odorico, P., Diekmann, L., DeLonge, M., Das, R., and Eaton, J. 2007. Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. Proceedings of the National Academy of Sciences of the United States of America 104:20696–20701.

Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. Oceanography and Marine Biology: an annual review 13:213–286.

Levins, R., 1998. Qualitative mathematics for understanding, prediction and intervention in complex ecosystems. Pages 178–204 *in* D. Rapport, R. Costanza, P. Epstein, C. Gaudet, and R. Levins, eds. Ecosystem Health, volume Chapter 11.

Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia 156:883–894.

Ling, S. D. and Johnson, C. R. 2009. Population dynamics of an ecologically important range-extender: kelp beds versus sea urchin barrens. Marine Ecology-Progress Series 374:113–125.

Ling, S. D. and Johnson, C. R. In press. Marine reserves reduce risk of climate-driven phase shift by reinstating size and habitat specific trophic interactions. Ecological Applications Doi: 10.1890/11-1587.1.

Ling, S. D., Johnson, C. R., Frusher, S., and King, C. K. 2008. Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. Global Change Biology 14:19.

Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. 2009*a*. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences of the United States of America 106:22341–22345.

Ling, S. D., Johnson, C. R., Ridgway, K., Hobday, A. J., and Haddon, M. 2009*b*. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Global Change Biology 15:719–731.

Linnane, A., Gardner, C., Hobday, D., Punt, A., McGarvey, R., Feenstra, J., Matthews, J., and Green, B. 2010. Evidence of large-scale spatial declines in recruitment patterns of southern rock lobster *Jasus edwardsii*, across south-eastern australia. Fisheries Research 105:163–171.

Lobban, C. S. and Harrison, P. J., 1996. Seaweed Ecology and Physiology. Cambridge University Press, New York.

Mace, P. 2001. A new role for msy in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries 2:2–32.

Mann, K. H. 1982. Kelp, sea urchins and predators - a review of strong-interactions in rocky subtidal systems of eastern canada, 1970- 1980. Netherlands Journal of Sea Research 16:414–423.

Marzloff, M., Shin, Y. J., Tam, J., Travers, M., and Bertrand, A. 2009. Trophic structure of the Peruvian marine ecosystem in 2000-2006: Insights on the effects of management

scenarios for the hake fishery using the IBM trophic model Osmose. Journal of Marine Systems 75:290–304.

Marzloff, M. P., Dambacher, J. M., Johnson, C. R., Little, L. R., and Frusher, S. D. 2011*a*. Exploring alternative states in ecological systems with a qualitative analysis of community feedback. Ecological Modelling 222:2651–2662.

Marzloff, M. P., Johnson, C. R., Little, L. R., Frusher, S. D., Ling, S. D., and Soulié, J.-C., 2011*b*. A management support framework for subtidal rocky-reef communities on the east coast of Tasmania.*in* F. Chan, D. Marinova, and R. Anderssen, eds. MODSIM2011: 19th International Congress on Modelling and Simulation., Pages 2142–2148. Modelling and Simulation Society of Australia and New Zealand. December 2011. http://www.mssanz.org.au/modsim2011/E9/marzloff.pdf.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

McClanahan, T. R., Graham, N. A. J., MacNeil, M. A., Muthiga, N. A., Cinner, J. E., Bruggemann, J. H., and Wilson, S. K. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences of the United States of America 108:17230–17233.

McGarvey, R. and Feenstra, J. E. 2001. Estimating length-transition probabilities as polynomial functions of premoult length. Marine and Freshwater Research 52:1517–1526.

Melbourne-Thomas, J., Johnson, C. R., Alino, P. M., Geronimo, R. C., Villanoy, C. L., and Gurney, G. G. 2010. A multi-scale biophysical model to inform regional management of coral reefs in the western philippines and south china sea. Environmental Modelling & Software 26:66–82.

Melbourne-Thomas, J., Johnson, C. R., and Fulton, E. A. 2011*a*. Characterizing sensitivity and uncertainty in a multiscale model of a complex coral reef system. Ecological Modelling 222:3320–3334.

Melbourne-Thomas, J., Johnson, C. R., and Fulton, E. A. 2011*b*. Regional-scale scenario analysis for the meso-american reef system: Modelling coral reef futures under multiple stressors. Ecological Modelling 222:1756–1770.

Metcalf, S. J., Dambacher, J. M., Hobday, A. J., and Lyle, J. M. 2008. Importance of trophic information, simplification and aggregation error in ecosystem models. Marine Ecology-Progress Series 360:25–36.

Metcalf, S. J., Pember, M. B., and Bellchambers, L. M. 2011. Identifying indicators of the effects of fishing using alternative models, uncertainty, and aggregation error. Ices Journal of Marine Science 68:1417–1425.

Miller, R. J. 1989. Catchability of American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) by traps. Canadian Journal of Fisheries and Aquatic Sciences 46:1652–1657.

Mohn, R. K. and Miller, R. J. 1987. A ration-based model of a seaweed sea-urchin community. Ecological Modelling 37:249–267.

Mumby, P. J., Hastings, A., and Edwards, H. J. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Murawski, S. A. 2000. Definitions of overfishing from an ecosystem perspective. ICES Journal of Marine Science: Journal du Conseil 57:649–658.

Novak, M. 2010. Estimating interaction strengths in nature: experimental support for an observational approach. Ecology 91:2394–2405.

Novak, M. and Wootton, J. T. 2008. Estimating nonlinear interaction strengths: An observation-based method for species-rich food webs. Ecology 89:2083–2089.

Nylund, G. M. and Pavia, H. 2005. Chemical versus mechanical inhibition of fouling in the red alga *Dilsea carnosa*. Marine Ecology-Progress Series 299:111–121.

Osman, R. W., Munguia, P., Whitlatch, R. B., Zajac, R. N., and Hamilton, J. 2010. Thresholds and multiple community states in marine fouling communities: integrating natural history with management strategies. Marine Ecology-Progress Series 413:277–289.

Overland, J., Rodionov, S., Minobe, S., and Bond, N. 2008. North Pacific regime shifts: Definitions, issues and recent transitions. Progress in Oceanography 77:92–102.

Overland, J. E., Alheit, J., Bakun, A., Hurrell, J. W., Mackas, D. L., and Miller, A. J. 2010. Climate controls on marine ecosystems and fish populations. Journal of Marine Systems 79:305–315.

Pecl, G., Frusher, S., Gardner, C., Haward, M., Hobday, A., Jennings, S., Nursey-Bray, M., Punt, A., Revill, H., and van Putten, I., 2009. The East Coast Tasmanian Rock Lobster Fishery - Vulnerability to climate change impacts and adaptation response options. Technical report, Report to the Australian Government Department of Climate Change.

Pederson, H. G., Barrett, N. S., Frusher, S. D., and Buxton, C. D. 2008. Effect of predator-prey and competitive interactions on size at emergence in the blacklip abalone *Haliotis rubra* in a Tasmanian MPA. Marine Ecology-Progress Series 366:91–98.

Petraitis, P. S. and Dudgeon, S. R. 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. Oikos 84:239–245.

Petraitis, P. S. and Dudgeon, S. R. 2004. Detection of alternative stable states in marine communities. Journal of Experimental Marine Biology and Ecology 300:343–371.

Polasky, S., Carpenter, S. R., Folke, C., and Keeler, B. 2011. Decision-making under great uncertainty: environmental management in an era of global change. Trends in Ecology & Evolution 26:398–404.

Puccia, C. J. and Levins, R., 1985. Qualitative Modeling of Complex Systems: An introduction to Loop Analysis and Time Averaging. Harvard University Press, Cambridge, Massachussets and London, England.

Punt, A. E. and Kennedy, R. B. 1997. Population modelling of Tasmanian rock lobster, *Jasus edwardsii*, resources. Marine and Freshwater Research 48:967–980.

Punt, A. E., Kennedy, R. B., and Frusher, S. D. 1997. Estimating the size-transition matrix for Tasmanian rock lobster, *Jasus edwardsii*. Marine and Freshwater Research 48:981–992.

Python Software Foundation, 2008. Python 2.6.1.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL `http://www.R-project.org/`.

Redd, K. S., Jarman, S. N., Frusher, S. D., and Johnson, C. R. 2008. A molecular approach to identify prey of the southern rock lobster. Bulletin of Entomological Research 98:233–238.

Redmap, 2010. http://www.redmap.org.au/.

Reed, D. C., Rassweiler, A., Carr, M. H., Cavanaugh, K. C., Malone, D. P., and Siegel, D. A. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92:2108–2116.

Ridgway, K. R. 2007*a*. Long-term trend and decadal variability of the southward penetration of the East Australian Current. Geophysical Research Letters 34.

Ridgway, K. R. 2007*b*. Seasonal circulation around Tasmania: An interface between eastern and western boundary dynamics. Journal of Geophysical Research-Oceans 112.

Running, S. W. 2008. Climate change - ecosystem disturbance, carbon, and climate. Science 321:652–653.

Saltelli, A., Campolongo, F., and Cariboni, J. 2009. Screening important inputs in models with strong interaction properties. Reliability Engineering & System Safety 94:1149–1155.

Saltelli, A., Tarantola, S., and Campolongo, F. 2000. Sensitivity analysis as an ingredient of modeling. Statistical Science 15:377–395.

Saltelli, A., Tarantola, S., and Chan, K. P. S. 1999. A quantitative model-independent method for global sensitivity analysis of model output. Technometrics 41:39–56.

Samhouri, J. F., Levin, P. S., and Ainsworth, C. H. 2010. Identifying thresholds for ecosystem-based management. Plos One 5:10.

Sanderson, J. C., 1990. Subtidal Macroalgal Studies In East and South Eastern Tasmanian Coastal Waters. Msc thesis, University of Tasmania.

Scheffer, M., Carpenter, S., and de Young, B. 2005. Cascading effects of overfishing marine systems. Trends in Ecology & Evolution 20:579–581.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B., and Jeppesen, E. 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution 8:275–279.

Scheffer, M., van Nes, E. H., Holmgren, M., and Hughes, T. 2008. Pulse-driven loss of top-down control: The critical-rate hypothesis. Ecosystems 11:226–237.

Schroder, A., Persson, L., and De Roos, A. M. 2005. Direct experimental evidence for alternative stable states: a review. Oikos 110:3–19.

Seitz, R. D., Lipcius, R. N., Hines, A. H., and Eggleston, D. B. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82:2435–2451.

Skalski, G. T. and Gilliam, J. F. 2001. Functional responses with predator interference: viable alternatives to the Holling Type II models. Ecology 82:3083–3092.

Smallegange, I. M. and van der Meer, J. 2010. Testing a stochastic version of the Beddington-DeAngelis functional response in foraging shore crabs. Marine Biology 157:1027–1040.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L. J., Shin, Y. J., and Tam, J. 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science 333:1147–1150.

Smith, A. D. M., Fulton, E. J., Hobday, A. J., Smith, D. C., and Shoulder, P. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. Ices Journal of Marine Science 64:633–639.

Sommer, U. 1999. The susceptibility of benthic microalgae to periwinkle (*Littorina littorea*, gastropoda) grazing in laboratory experiments. Aquatic Botany 63:11–21.

Soulé, C. 2003. Graphic requirements for multistationarity. ComPlexUs 1:123–133.

Steneck, R. S., Vavrinec, J., and Leland, A. V. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems 7:323–332.

Strain, E. M., 2009. The indirect effects of fishing blacklip abalone *Haliotis rubra*. Phd thesis, University of Tasmania.

Strain, E. M. A. and Johnson, C. R. 2010. Scale-dependent relationships between benthic habitat characteristics and abundances of blacklip abalone, *Haliotis rubra* (leach). Marine and Freshwater Research 61:1227–1236.

Strain, E. M. A. and Johnson, C. R. 2012. Intensive fishing of marine consumers causes a dramatic shift in the benthic habitat on temperate rocky reefs. Marine Biology 159:533–547.

Strain, E. M. A. and Johnson, C. R. In press. Intensive fishing of abalone causes a shift to benthic habitat types poorly preferred by abalone. Ecology .

Suding, K. N., Gross, K. L., and Houseman, G. R. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46–53.

Suding, K. N. and Hobbs, R. J. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution 24:271–279.

Sutherland, W. J., Adams, W. M., Aronson, R. B., Aveling, R., Blackburn, T. M., Broad, S., Ceballos, G., Cote, I. M., Cowling, R. M., Da Fonseca, G. A. B., Dinerstein, E., Ferraro, P. J., Fleishman, E., Gascon, C., Hunter, M., Hutton, J., Kareiva, P., Kuria, A., MacDonald, D. W., MacKinnon, K., Madgwick, F. J., Mascia, M. B., McNeely, J., Milner-Gulland, E. J., Moon, S., Morley, C. G., Nelson, S., Osborn, D., Pai, M., Parsons, E. C. M., Peck, L. S., Possingham, H., Prior, S. V., Pullin, A. S., Rands, M. R. W., Ranganathan, J., Redford, K. H., Rodriguez, J. P., Seymour, F., Sobel, J., Sodhi, N. S., Stott, A., Vance-Borland, K., and Watkinson, A. R. 2009. One hundred questions of importance to the conservation of global biological diversity. Conservation Biology 23:557–567.

Thomas, R. 1981. On the relation between the logical structure of systems and their ability to generate multiple steady states or sustained oscillations. Springer Series in Synergetics 9:180–193.

Thomson, J. D., Weiblen, G., Thomson, B. A., Alfaro, S., and Legendre, P. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. Ecology 77:1698–1715.

Turley, M. C. and Ford, E. D. 2009. Definition and calculation of uncertainty in ecological process models. Ecological Modelling 220:1968–1983.

Valdivia, J. E. G. 1978. The anchoveta and El Nino. Rapp. et P.-v. Reun. Cons. int. Explor. Mer. 173:196–202.

Valentine, J. P. and Johnson, C. R. 2005. Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. Marine Ecology-Progress Series 285:43–55.

van de Koppel, J., Rietkerk, M., and Weissing, F. J. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology & Evolution 12:352–356.

van der Meer, J. and Smallegange, I. M. 2009. A stochastic version of the Beddington-De Angelis functional response: modelling interference for a finite number of predators. Journal of Animal Ecology 78:134–142.

van Nes, E. H. and Scheffer, M. 2003. Alternative attractors may boost uncertainty and sensitivity in ecological models. Ecological Modelling 159:117–124.

van Nes, E. H. and Scheffer, M. 2004. Large species shifts triggered by small forces. American Naturalist 164:255–266.

Walters, C. J., Christensen, V., Martell, S. J., and Kitchell, J. F. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessments. Ices Journal of Marine Science 62:558–568.

Wernberg, T. 2005. Holdfast aggregation in relation to morphology, age, attachment and drag for the kelp *Ecklonia radiata*. Aquatic Botany 82:168–180.

Wong, M. C. and Barbeau, M. A. 2006. Rock crab predation of juvenile sea scallops: the functional response and its implications for bottom culture. Aquaculture International 14:355–376.

Wong, M. C., Peterson, C. H., and Kay, J. 2010. Prey size selection and bottom type influence multiple predator effects in a crab-bivalve system. Marine Ecology-Progress Series 409:143–U158.

Wright, J. T., Dworjanyn, S. A., Rogers, C. N., Steinberg, P. D., Williamson, J. E., and Poore, A. G. B. 2005. Density-dependent sea urchin grazing: differential removal of species, changes in community composition and alternative community states. Marine Ecology-Progress Series 298:143–156.

Zabel, R. W., Harvey, C. J., Katz, S. L., Good, T. P., and Levin, P. S. 2003. Ecologically sustainable yield: Marine conservation requires a new ecosystem-based concept for fisheries management that looks beyond sustainable yield for individual fish species. American Scientist 91:150–157.